THE Ds LOCUS

PART III. TRANSPOSITION OF THE Ds LOCUS. April, 1949

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April, 1949

The Ds locus. Part III. Transposition of the Ds locus.

Outline

THE Ds LOCUS. PART III. TRANSPOSITION OF THE Ds LOCUS

1. Introduction

Transposition of the Ds locus is a relatively frequent phenomenon. In the report on the origin and behavior of the c-ml locus, it was shown that c-ml arose from a normal C locus as the consequence of a transposition of a Ds locus from its standard location in chromosome 9 to a position close to or within the C locus. The presence of the transposed Ds locus did not produce any alteration in the appearance of the chromosome in the region where it had been inserted, nor did its presence cause any reduction in crossing-over between C and Sh. In this new location, Ds responded to Ac in exactly the same way that it responds to Ac when in its standard location. The relation of this response to the production of visible mutations of c-ml to C was discussed in the earlier report. The study of c-ml mutational phenomena suggested that the Ac-controlled mutable loci arise because of transpositions of the Ds locus. Since these transpositions are relatively frequent, it may readily be understood why so many new Ac-controlled mutable loci are arising in the Ds, Ac plants and why previously stable "wild-type" loci "suddenly" become unstable and mutable.

Because transpositions of Ds are related to the origin of mutable loci, it is of prime importance to determine the mechanism responsible for this transposition. How does it occur and why does it occur with such relatively high frequencies? An extensive analysis of one case of transposition of Ds has indicated the probable mechanism that brings about this transposition. The analysis also suggests the reason why these transpositions are so frequent. This case of transposition of Ds will be considered in detail in this report.

2. The origin of transposed Ds, Case I

The first recognized case of transposition of Ds arose in the cross of a plant (4108C-1) having the constitution wd I Sh Bz Wx Ds in one normal chromosome 9 and Wd C sh bz wx ds in a normal homologous chromosome 9. This plant was heterozygous for Ac (Ac ac). The types of kernels resulting from the cross of this plant to a female plant carrying C sh bz wx ds ac are given in table 1. (The male parent plant (4108C-1) arose from an I - C bz, Sh - sh, Wx-wx kernel on an ear coming from the cross of a C sh bz wx ds ac female plant by an Ac ac male plant having two normal chromosomes 9 with Wd C Sh Bz Wx Ds and wd I Sh Bz Wx ds, respectively. The kernel from which plant 4108C-1 arose was selected because it had received an I Sh Bz Wx Ds chromosome. The Ds locus was introduced into this chromosome as a consequence of crossing-over in the heterozygous male parent.) As table 1 shows, with the exception of two aberrant kernels, the types of kernels and the ratios obtained are those expected on the basis of the above given constitution of this plant. When this plant was crossed to a c sh Bz wx ds ac female plant, the types of kernels appearing on the ear are those given in table 2. The ratios of the various types of kernels obtained in this cross likewise agree with the given genic constitution of the male parent plant (4108C-1; see supplement to table 2). In both crosses, the variegation in those kernels having both Ds and Ac is of the

Table 1

Types of kernels appearing on ear from cross of

$$\text{C sh bz wx ds ac} \; ♀ \quad x \quad \frac{\text{I Sh Bz Wx Ds}}{\text{C sh bz wx ds}} \; \text{Ac ac} \; ♂$$

Plant 4108C-1

Kernel type	Number of kernels	
I-C bz, Sh*, Wx-wx	57	
I Sh Wx	59	
C sh bz wx	128	
I sh wx	5	
C Bz-C bz, Sh, Wx-wx	5	
C Sh Bz Wx	2	
I Sh wx	52	
C Bz-C bz, sh, Wx-wx	0	
C sh Bz Wx	1	
C sh bz, Wx-wx	22	
C sh bz Wx	31	
I-C Bz-C bz, Sh, Wx-wx	1	Origin of Plant 4306
I-C Bz, Sh wx	1	Not tested
Totals	364	

* The Sh-sh variegation will not be indicated in the table. It may be understood to be present.

Supplement to Table 1

Types of chromatids produced by plant 4108C-1 and appearance of kernel in table 1

1	2		3	4		
I	Sh	Bz		Wx	Ds	
						Ac ac
C	sh	bz		wx	ds	

			Appearance of kernel	
Non Cross-over chromatids	I Sh B bz Wx Ds	Ac	I-C bz, Sh-sh, Wx-wx	57
		ac	I Sh Wx	
	C sh bz wx ds	Ac and ac	C sh bz wx	
Region 1	I sh bz wx ds	Ac and ac	I sh wx	5
	C Sh Bz Wx Ds	Ac	C Bz-C bz, Sh-sh, Wx-wx	5
		ac	C Sh Bz Wx	2
Region 2	I Sh bz wx ds	Ac and ac	I Sh wx	
	C sh Bz Wx Ds	Ac	C Bz-C bz, sh, Wx-wx	0
		ac	C sh Bz Wx	1
Region 3	I Sh Bz wx ds	Ac and ac	I Sh wx	
	C sh bz Wx Ds	Ac	C sh bz Wx-wx	22
		ac	C sh bz Wx	31
Region 4	I Sh Bz Wx ds	Ac and ac	I Sh Wx	
	C sh bz wx Ds	Ac and ac	C sh bz wx	

Observed double cross-over, Regions 2 and 3 :-1 C sh Bz wx non-variegated

Odd classes = 2. See Table 1.

Table 2

Types of kernels appearing on ear from cross of

$$c\ sh\ Bz\ wx\ ds\ ac\ ♀ \quad x \quad \frac{I\ Sh\ Bz\ Wx\ Ds}{C\ sh\ bz\ wx\ ds}\ Ac\ ac\ ♂$$

Plant 4108C-1

Kernel type	Number of kernels
I-C Bz, Sh*, Wx-wx	41
I Sh Wx	68
C sh wx	86
I sh wx	4
C-c, Sh, Wx-wx	3
C Sh Wx	1
I Sh wx	48
C-c, sh, Wx-wx	14
C sh Wx	24
I sh Wx	1
Totals	290

162 I : 128 C
152 Wx : 138 wx

* The Sh-sh variegation will not be indicated in the table but may be understood to be present.

Supplement to Table 2

Chromatids produced by plant 4108C-1 and appearance of kernels:

Cross-over regions tested:

I Sh Wx Ds

C sh wx ds

1 2 3

Cross-over region	Constitutions of ♂ gametes		Resulting kernel type	Critical kernels
Non-crossovers	I Sh Wx Ds	Ac	I-c Sh Wx-wx	41
		ac	I Sh Wx	
	C sh wx ds	Ac and ac	C sh wx	
Region 1	I sh wx	Ac and ac	I sh wx	4
	C Sh Wx Ds	Ac	C-c Sh Wx-wx	3
		ac	C Sh Wx	1
Region 2	I Sh wx ds	Ac and ac	I Sh wx	48
	C sh Wx Ds	Ac	C-c sh Wx-wx	14
		ac	C sh Wx	24
Region 3	I Sh Wx ds	Ac and ac	I Sh Wx	
	C sh wx Ds	Ac	C-c sh wx	0
		ac	C sh wx	

Regions 1 and 2: 1 I sh Wx (Ds ac).

type expected when a Ds locus is at its standard position in the I Sh Bz Wx chromosome. The Ds mutations gave rise to C sh bz wx sectors (table 1) or c sh wx sectors (table 2). Also, the position of this Ds locus is obvious from the types and frequencies of recovered cross-over chromatids shown in tables 1 and 2. There can be no doubt that in plant 4108C-1, Ds was located to the right of Wx,--at its standard location in the wd I Sh Bz Wx chromosome.

One of the two exceptional kernels listed in table 1 showed a type of variegation that would not arise from an I Sh Bz Wx Ds order of genes. In this kernel, many chromosome breaks of the Ds mutational type had occurred, but the position of the breaks was just to the right of the I locus instead of to the right of the Wx locus. These breaks gave rise to cells in which the I locus was eliminated but the Sh Bz and Wx loci were retained. Following such a Ds mutation, a dicentric chromatid was formed that had Sh Bz and Wx in the short arms of the two terminally fused chromatids (the dicentric chromatid). Continued breakage-fusion-bridge cycles resulted in successive deletions of these loci in some of the descendent cells. Consequently, within the C Bz Wx sector sub-sectors of bz w+ and bz wx were present. Another type of variegation was also present but the description of the variegation types will be postponed until later when correlations of the genic organization of this chromosome with the variegation patterns can logically be derived.

The aberrant kernel was planted in the greenhouse in the winter of 1947-48. No cytological examination was made of the plant arising from this kernel for fear of injury. Because the plant was very early in maturing and because no other plants were available for crossing, only a self-pollination of this plant was possible. The types of kernels appearing on this self-pollinated ear are given in table 3. The chromosomal and genic constitution of the aberrant chromosome 9 carrying I Sh Bz Wx in this plant has been determined from an analysis of the plants arising from the kernels on this self-pollinated ear. This analysis makes the types of kernels that appeared on the ear readily interpretable. Because the kernels are quite different from those arising in previous studies, a supplementary analysis giving the chromatids that could be produced during meiosis in this plant and the types of gametes that will result accompanies table 3. This plant had a normal chromosome 9 carrying C ds sh bz wx ds and a Duplication chromosome 9 with wd ~~and~~ I, ~~and~~ Sh Bz Wx was carried in each of the two duplicated segments (see diagram, table 3 supplement). Synapsis between the two chromosomes 9 usually occurs as given in the diagram and the crossover percentages between the marked loci are not reduced, as the genetic analysis of the F_2 plants that were heterozygous for this duplication will show. The "ds" designation is meaningless with respect to the presence of any true allelic loci. It has been inserted to make the constitutions easier to read at a glance. Because of the many possible classes of crossover chromatids that could arise in this plant, only the single crossovers between the two chromosomes 9 following synapsis of the distal duplicated segment in the Duplication chromosome 9 with its homologous segment in the normal chromosome 9 are given in the supplement to table 3. Double crossovers in the region between C and wx are relatively rare and will be neglected at this point in the discussion. The single crossovers, however, are frequent and are most important in interpreting the constitutions of the observed types of kernels. Although it was realized from the types of kernels on the self-pollinated ear that

Table 3

Types of kernels appearing on self-pollinat~~ion~~ed ear of Plant 4306

Constitution:

wd I Ds' Sh Bz Wx Wx Bz Sh Ds²

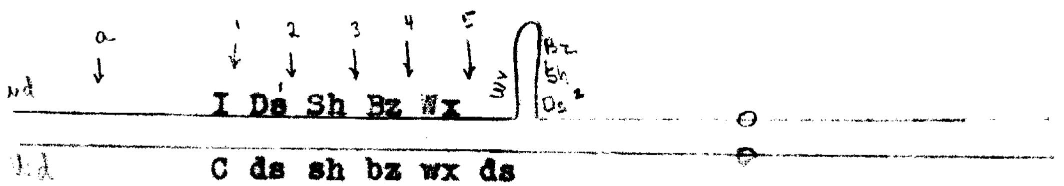
Wd C ds sh bz wx ds

Ac ac

I kernels		C kernels	
I Sh Wx	81	C Sh Bz Wx	4
I Sh Wx-wx	6	C Bz-C bz, Sh-sh, Wx-wx	3
I-C Bz-C bz, Sh-sh, Wx-wx	73	C sh bz wx	89
I-C Bz, Sh Wx	1		
I Sh wx	4	Total : 274	
I-C Bz-C bz, Sh-sh, wx	10	178 I : 96 C	
I sh wx	2	168 Wx : 106 wx	
I bz-C bz, sh wx	1		

Supplement to Table 3

Types of chromatids produced by plant 4306. Non-crossover and single cross-over chromatids resulting from the usual type of synapsis. The expected appearance of the kernel if combined with a C sh bz wx ds chromosome in Ac ac ac or ac ac ac constitution



Chromatids			Appearance of kernel
Non-crossovers	I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	C ds sh bz wx ds normal	Ac and ac	C sh bz wx
	I ds sh bz wx ds normal	Ac and ac	I sh wx
Region 1	C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 2	I Ds^1 sh bz wx ds normal	Ac	I bz-C bz, sh wx
		ac	I sh wx
	C ds Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx

Supplement to Table 3 continued

Region 3	I Ds^{1} Sh bz wx ds normal	Ac	I bz-C bz, Sh wx
		ac	I Sh wx
	C ds sh Bz Wx Wx Bz Sh Ds^{2} Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 4	I Ds^{1} Sh Bz wx ds normal	Ac	I-C Bz-C bz, Sh wx
		ac	I Sh wx
	C ds sh bz Wx Wx Bz Sh Ds^{2} Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region 5	I Ds^{1} Sh Bz Wx ds normal	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	C ds sh bz wx Wx Bz Sh Ds^{2} Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Region a Not considered in table	Wd I Ds^{1} Sh Bz Wx Wx Bz Sh Ds^{2} Duplication	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	wd C ds sh bz wx ds normal	Ac and ac	C sh bz wx

(1) a Ds locus had been transposed just to the right of the I locus and that (2) some chromosomal aberration involving the region to the right of the I locus had likewise occurred, the exact nature of the aberration was not clearly understood from the analysis of this ear alone.

To obtain exact information on the aberration that occurred and its possible relation to a transposition of Ds, some of the kernels in the various classes represented in table 3 were planted in the summer of 1948 under culture number 4628. With respect to Wd or wd and Bz or bz, the types of plants arising from these various classes of kernels are given in table 4.

3. <u>Cytological examination of plants in culture 4628</u>.

Cytological examination was made of a number of plants in the various sub-classes of culture 4628. The sporocytes in some of these plants gave very poor figures. Those in which the constitution of chromosome 9 was clear and readily analyzable are summarized in table 5. In sub-cultures D and E, the majority of plants probably had the same genic as well as chromosomal constitution as the mother plant. All the examined plants had one normal chromosome 9 and a chromosome 9 with a duplication of a mid-segment of the short arm. This duplicated segment was inserted into the short arm. Homologous synaptic association of the short arm of the normal chromosome 9 with the short arm of the Duplication chromosome 9 usually occurred along the distal two-thirds of the arm. A loop configuration in the Duplication chromosomes 9 was present. Its position varied in the different sporocytes but it was usually close to or within the deep-staining region adjacent to the centromere. None of this proximal

Table 4

Appearance of plants in culture 4628 obtained from selected ~~groups of~~ kernels on self-pollinated ear of plant 4306 (table 3)

Sub-culture designations	Appearance of kernel in each sub-culture from which plants arose	Number of kernels planted	Appearance of plants arising from kernels	
A	I-C Bz, Sh Wx	1	0	No shoot developed; only roots
B	I Sh Wx-wx	2	2	white seedlings (wd/wd)
C	I Sh Wx	20	17	Wd, Bz : 1 white : 2 no germination
D	I-C Bz-C bz, Sh-sh, Wx wx (Many C bz wx areas)	15	15	Wd, Bz
E	I-C Bz-C Bz, Sh-sh, Wx-wx (Few C bz wx areas)	10	8	Wd, Bz : 1 white : 1 no germination
F	I Sh wx	2	2	Wd, Bz
G	I-C Bz-C bz, Sh-sh, wx (Many C bz areas)	3	3	Wd, Bz
H	I-C Bz, Sh-sh, wx (Few C bz areas)	2	2	Wd, Bz
I	I sh wx	2	2	Wd, bz
J	I bz-C bz, sh wx	1	1	Wd; died in seedling stage
K	C Sh Bz Wx	2	2	Wd, Bz
L	C Bz-C bz, Sh-sh, Wx-wx	2	2	Wd, Bz
M	C sh bz wx	20	6	Wd, bz

Table 5

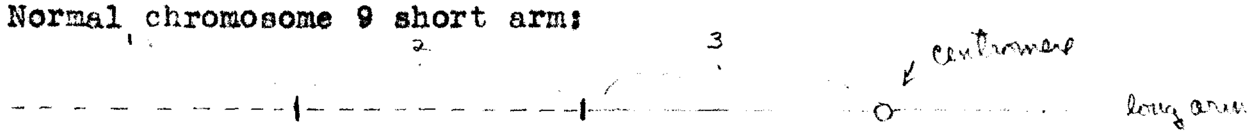
Constitutions of chromosomes 9 in plants of culture 4628 based upon examination of sporocytes at pachytene.

Plant Number	Constitution of chromosomes 9 in examined plant	Constitution of plant from pollen examination
4628C- 9	2 Duplications chromosomes 9	Wx Wx
4628C-17	1 Duplication chromosome 9 1 Normal " "	Wx wx
4628D-10	1 Duplication " " 1 Normal " "	Wx wx
4628D-11	1 Duplication " " 1 Normal " "	Wx wx
4628D-12	1 Duplication 1 Normal	Wx wx
4628E- 8	1 Duplication 1 Normal	Wx wx
4628F- 1	2 Normal	wx wx
4628F- 2	2 Normal	wx wx
4628G- 1	2 Normal	wx wx
4628G- 2	2 Normal	wx wx
4628H- 1	2 Normal	wx wx
4628H- 2	2 Normal	wx wx
4628L- 1	1 Duplication 1 Normal	Wx wx

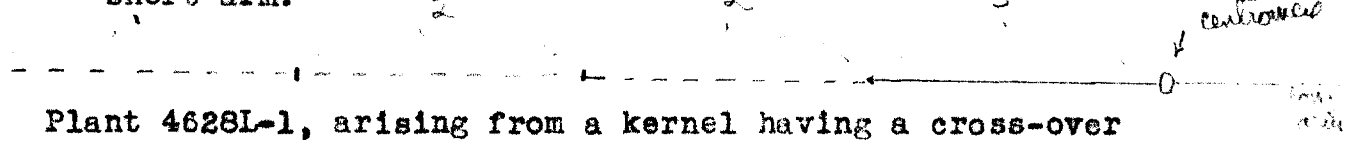
deep-staining region, however, was included in the duplicated segment.

Plant 4628C-9 was homozygous for the chromosome 9 with the duplication. By comparative measurements of the short and long arms of chromosome 9 in this plant and from the appearance of the chromomeres within this arm, it was apparent that the duplication was composed of a segment approximately equivalent in length to a third of the normal short arm. It was composed only of the smaller chromomeres characteristic of the distal two-thirds of the normal short arm. It was concluded (1) from the chromomere constitution in the plant homozygous for this duplication, (2) from the synaptic phenomena in the heterozygous plants and (3) from the genic and chromosomal constitutions of the F_2 population that the duplicated segment was composed of a section of the middle of the short arm of chromosome 9 and of a length approximately one-third of this arm. This segment had been inserted into a normal short arm. This may be diagrammed, without reference to order of genes, as follows:

Normal chromosome 9 short arm:



Duplication chromosome 9
short arm:



Plant 4628L-1, arising from a kernel having a cross-over chromatid, was heterozygous for the Duplication chromosome 9. Synaptic behavior between the normal and the Duplication chromosome 9 was similar to that described for the heterozygous plants in sub-cultures D and E. The plants in sub-cultures F, G and H, on the other hand, had two morphologically normal chromosomes 9. No abnormalities of any kind could be seen in the chromosomes 9 of these plants. In all of these plants, however, the I, Ds, Sh and Bz loci in the normal chromosome 9 had originally been located in the Duplication chromosome 9 of the mother plant.

A genetic analysis of the plants of culture 4628 has made it possible to state (1) the genic composition of the two identical segments in the Duplication chromosome 9, (2) the order of the genes in each segment and (3) the probable event that occurred in a cell of plant 4108C-1 which produced the duplication and the transposition of a Ds locus from its standard position to a position immediately to the right of the I locus. The purpose of the following description is to give the evidence that allows these conclusions to be drawn.

4. The genetic analysis of the plants in culture 4628. (a). Sub-culture C.

Pollen examinations were made of a number of plants of culture 4628 (table 6). This was particularly important in sub-culture C in order to select those plants that could be expected to be homozygous for the Duplication chromosome 9. These plants should be Wx Wx. Only 3 Wx Wx plants were present in this sub-culture. Because plant C-9, a Wx Wx plant, had also been examined cytologically, it was selected for tests to determine the types of variegation patterns that the Ds loci in the Duplication chromosomes 9 would produce. This plant was crossed to the following female plants:

Table 6

Wx and wx constitutions in plants of culture 4628 based on pollen examination

Sub-culture	Wx Wx*	Wx wx	wx wx	Appearance of kernels from which plant arose
C	3	14	0	I Sh Wx
D	0	3	0	I - C Bz - C bz, Sh-sh, Wx-wx
E	0	1	0	I - C Bz - C bz, Sh-sh, Wx-wx (few C bz areas)
F	0	0	2	I Sh wx
G	0	0	3	I - C Bz - C bz, Sh-sh, [illegible]-wx
H	0	0	2	I - C Bz, Sh-sh, wx (few C bz areas)
I	0	0	2	I sh wx
K	0	2	0	C Sh Bz Wx
L	0	2	0	C Bz - C bz, Sh-sh, Wx-wx

* All 3 plants had a few, small, partially filled wx staining pollen grains. This is to be expected from Ds^2 mutations (see Annual Report, 1948).

(1) C sh bz wx ds, ac ac

(2) C sh bz wx ds, Ac ac

(3) c sh Bz wx ds, ac ac

(4) C Sh Bz wx Ds / C Sh Bz wx Ds, Ac Ac

(5) C Sh Bz wx Ds / C Sh Bz wx Ds, ac ac

When crossed to C sh bz wx ds ac female plants, two types of kernels appeared on the ears in equal ratios. One was I Sh Wx and non-variegated. The other type of kernel was variegated (table 7-a). All these variegated kernels had sectors that had lost the I locus. Many of the sectors were C Bz Wx in phenotype but within the sector variation for C bz was present. These C bz areas were all wx. Within the C Bz sectors there were often large wx areas that were definitely Bz and not bz. This is important, as will be indicated later. There were also some C bz wx sectors, not within or associated with the C Bz sectors. It was evident that two types of events were occurring in these kernels. Both involved loss of the I locus but one gave the C Bz Wx sectors with C bz wx and Bz wx areas within them and one gave C bz wx sectors directly. Further analysis has made it clear that these two separate types of variegation are associated with the presence of two Ds loci in the Duplication chromosome 9, one (Ds^1) located just to the right of the I locus and one (Ds^2) located to the right of the proximal duplicated segment. A Ds^2 mutation accounts for the appearance of the independent C bz wx sectors; a Ds^1 mutation gives rise to the C Bz Wx sectors with a secondary type of variegation within them, as described above; (produced by breakage - fusion - bridge cycles following the formation of the dicentric chromatid from a Ds^1 mutation).

Table 7-a

$$C\ sh\ bz\ wx\ ds\ ac\ ♀ \times \frac{I\ Ds^1\ Sh\ Bz\ Wx\ Wx\ Bz\ Sh\ Ds^2}{I\ Ds^1\ Sh\ Bz\ Wx\ Wx\ Bz\ Sh\ Ds^2}\ Ac\ ac\ ♂$$

Plant 4628C-9

	Kernel types	
Cross	I Sh Wx	I-C Bz-C bz; Sh-sh, Wx-wx*
4361-5 x 4628C-9	222	212
4363-10 x " "	18	16
4362C-6 x " "	273	236
Totals	513	464

* See text for accurate description of variegation.

Table 7-b

c sh bz wx ds ac ♀ x 4628C-9 ♂

Cross	Kernel types Colorless Sh Wx	 Colorless Sh-sh Wx-wx
4347-19 x 4628C-9	180	189

Table 7-c

C sh bz wx ds, Ac ac ♀ x 4628C-9

Cross	I Sh Wx* not obviously variegated (Ac Ac Ac and ac ac ac)	I-C Bz-C bz, sh-abr Wx-wx		Odds
		Speckled (Ac Ac ac)	Ac ac ac type	
4462C-11 x 4628C-9	190	121	140	
4462C-1 x " "	171	115	110	1 C Sh Bz Wx non-varie-gated *
Totals	361	236	250	1

* Some of the kernels in this column have a few small C areas or a few specks of C.

* Contamination See 4876B, summer 1947 = [illegible]

[illegible]

Table 7-d

C Sh Bz wx Ds / C Sh Bz wx Ds, Ac Ac ♀ x 4628C-9 ♂

Cross	I Wx not obviously variegated (Ac Ac Ac)	I-C, Wx-wx Ac Ac ac type	I-C, Wx-wx Ac ac ac * type
4380B-6 x 4628C-9	25	36	1

* See report on Ac locus for explanation of this type of variegated kernel

The evidence obtained from this cross alone is not sufficient to establish the genic constitutions of the chromosomes 9 in this plant (4628C-9) as given in table 7-a. The analysis of the other plants in culture 4628 allows the genic constitutions of the chromosomes 9 in this plant to be designated with a high degree of certainty. The constitution of the Duplication chromosomes 9 are, then:
I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2.

That no C locus was present in the duplication chromosome 9 was indicated from the cross of 4628C-9 to c sh Bz wx ds ac female plants (table 7-b). All of the kernels resulting from this cross were colorless. No colored spots or areas were seen in any of them. Half of them, however, were Wx - wx variegated, as expected. If a C locus had been present to the right of Ds^1, then its presence should have been detected in the Wx - wx variegated kernels on this ear. It seems reasonable to conclude, therefore, that no C locus was present in the Duplication chromosome 9. That none should be present will be indicated when the projected event that gave rise to the duplication is discussed.

Plant 4628C-9 was crossed to a C sh bz wx ds, Ac ac female plant, table 7-c. If plant 4628C-9 were Ac ac in constitution, as the evidence in tables 7-a and 7-b indicate, the endosperm constitutions of the kernels represented in table 7-c should be 1 Ac Ac Ac : I Ac Ac ac : 1 Ac ac ac : 1 ac ac ac. Responses of the Ds loci to Ac dosage would determine the classes of kernels appearing on this ear. The ratios of classes, with respect to variegation pattern, in table 7-c, are those that could be anticipated. The observations suggest that some of the Ac Ac Ac constitutions allow a very light speckled pattern of variegation to appear--a few very late Ds mutations were occurring in some of these kernels. Table 7-d gives the types of kernels obtained from the cross of 4628C-9 to a C Sh Bz wx Ds C Sh Bz wx Ds, Ac Ac (allelic positions) female plant. Again, the classes of kernels appearing on the ear following this cross are in agreement with the projected constitution of the male parent.

(b). <u>Sub-culture D</u>

The tested plants in sub-culture D were all heterozygous for the Duplication chromosome 9. The selection of this class of kernels from the self-pollinated ear of plant 4306, would suggest that they might have similar chromosome and genic constitutions as the mother plant. Two of these plants were crossed to C sh bz wx ds ac female plants. The results of these crosses are given in table 8. Because of the many classes of kernels that could appear following this cross, a supplement to table 8 has been included to show the types of chromatids that these plants could produce, if they had the given chromosome 9 constitutions. The types of chromatids are the same as those that have been considered for the parent plant. (Supplement to table 3). In these crosses, however, a direct test for the presence of these various types of non-crossover and crossover chromatids is available. It may be seen from the supplement to table 8 that crossing over would produce morphologically normal chromosomes 9 having a transposed Ds locus. The constitutions of these chromosomes, in the single cross-over classes, would be: I Ds' sh bz wx, I Ds' Sh bz wx and I Ds' Sh Bz wx. The variegation pattern that each of these chromosomes would produce in the cross to C sh bz wx ds is apparent. They appear in table 8 under the designated headings I bz-C bz, sh, wx, I bz-C bz, Sh-sh, wx and I-C Bz-C bz, Sh-sh, wx, respectively. If plants

Table 8

C sh bz wx ds ac ♀ x $\frac{\text{I } Ds^1 \text{ Sh Bz Wx Wx Bz Sh } Ds^2}{\text{C ds sh bz wx ds}}$ Ac ac ♂

Kernel type	Cross 4363-6 x 4628D-10	4363-11 x 4628D-10	4363-17 x 4628D-11	4462C-8 x 4628D-11	Totals
I Sh Wx	38	55	37	70	200
I-C Bz-C bz, Sh*, Wx-wx	16	27	40	59	142
I Sh wx	22	29	13	30	94
I-C Bz-C bz, Sh, wx	8	16	19	33	76
I bz-C bz, Sh, wx	1	1	1	0	3
I sh wx	3	5	2	8	18
I bz-C bz, sh wx	1	3	2	6	12
C Sh Bz Wx	20	16	16	27	79
C Bz-C bz, Sh, Wx-wx	10	7	7	19	43
C Sh Bz wx	0	0	1	2	3
C sh bz wx	67	115	108	210	500
				Total kernels	1170

* The Sh-sh variegation will not be indicated in the table but may be understood to be present.

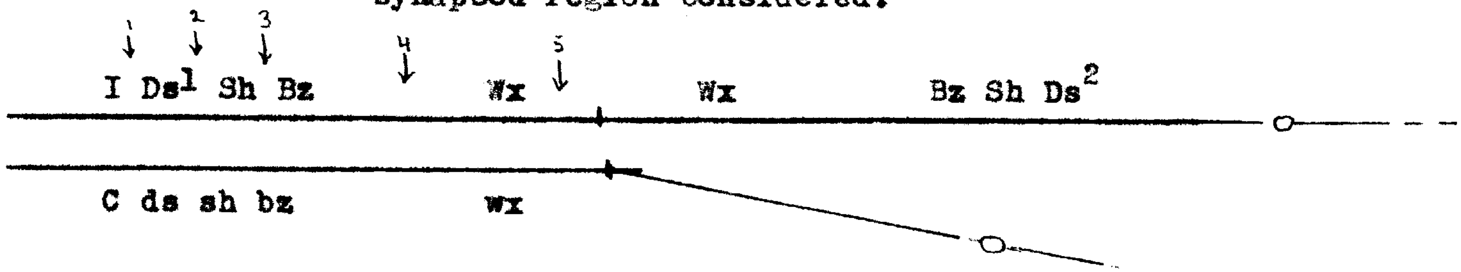
545 I : 625 C

385 Wx : 785 wx

4628D

Supplement to Table 8

Types of chromatids produced by ♂ plants in table 8. Only single cross-overs in designated synapsed region considered.



			Appearance of kernel in Table 8
Non-crossovers	I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Wx
	C ds sh bz wx ds normal	Ac and ac	C sh bz wx
Cross-overs Region 1	I ds sh bz wx ds normal	Ac and ac	I sh wx
	C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Crossovers Region 2	I Ds^1 sh bz wx ds Normal	Ac	I bz-C bz, sh wx
		ac	I sh wx
	C ds Sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx

Supplement to Table 8 continued

Crossovers Region 3	I Ds^1 Sh bz wx ds Normal	Ac	I bz-C bz, Sh, wx
		ac	I Sh wx
	C ds sh Bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Crossovers Region 4	I Ds^1 Sh Bz wx ds Normal	Ac	I-C Bz-C bz, Sh, wx
		ac	I Sh wx
	C ds sh bz Wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx
Crossovers Region 5	I Ds^1 Sh Bz Wx ds Normal	Ac	I-C Bz-C bz, Sh, Wx-wx
		ac	I Sh Bz Wx
	C ds sh bz wx Wx Bz Sh Ds^2 Duplication	Ac	C Bz-C bz, Sh, Wx-wx
		ac	C Sh Bz Wx

were grown from these kernels, all should possess two normal chromosomes 9. The selection of the C Bz - C bz, Sh - sh, Wx - wx kernels, on the other hand, should give rise to plants with a normal chromosome 9 carrying C sh bz wx ds and a Duplication chromosome 9 with the various constitutions indicated in the supplement to table 8. Because the region between Bz and Wx is the longest, the most frequent of the cross-over classes should be: normal chromosomes 9 with I Ds^1 Sh Bz wx and Duplication chromosomes 9 with C ds sh bz Wx Wx Sh Ds^2 (crossover region 4, supplement to table 8). Crossing over ratios may be determined in regions 2, 3 and 4 by comparing the frequencies of the various classes of I kernels showing variegation. The numbers in the I bz - C bz, sh wx class, (region 2), the I bz - C bz, Sh-sh, wx class (region 3) and the I - C Bz - C bz, Sh-sh, wx class (region 4) are 12 : 3 : 76, respectively. The crossover units for regions I to Sh, Sh to Bz and Bz to Wx in normal chromosomes 9 are approximately 3 : 2 : 21, respectively. The agreement in the two cases in relative frequencies in the several crossover regions is close. No serious disturbance in the <u>relative</u> frequencies of crossing-over in these regions is occurring in the plants that are heterozygous for the duplication.

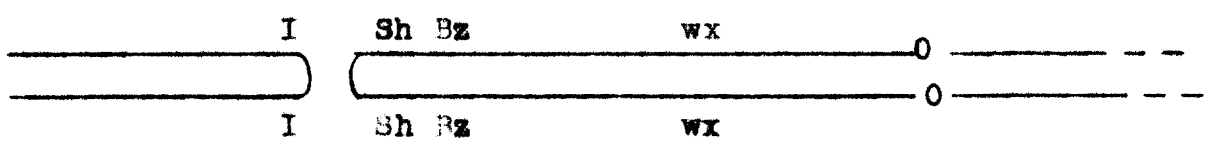
Moreover to test the projected constitutions of the gametes produced by plants 4628D-10 and 11 (table 8) it would be necessary to grow plants from the various classes of kernels in this table and test the chromosomal and genic constitutions of the chromosome 9 contributed by the male parent. Because the constitutions of the chromosome 9 in the gametes of the mother plant (4306) were probably the same as those produced by the two tested plants of sub-culture D, the probable constitutions of the plants in sub-cultures F to L can be anticipated.

On the self-pollinated ear of plant 4306 (table 3), the various crossover classes of kernels of the types indicated in table 8 were likewise present. The chromosome 9 constitutions of the examined plants arising from a selected number of such kernels has been given in table 5. The correspondence of chromosome constitution with expectancy on the basis of the selection was confirmed by the cytological analyses. Plants in sub-cultures G and H of culture 4628 should carry two normal chromosomes 9, one with I Ds' Sh Bz wx and one with C ds sh bz wx. These plants should be Ac ac, as the type of variegation observed in the kernels from which they arose would suggest. The plants in sub-culture F should have the same two chromosomes as plants in sub-cultures G and H but these plants could be either Ac Ac or ac ac. The plants in culture I, not examined cytologically, could be expected to have two normal chromosomes 9, one with I Ds' sh bz wx (an I ds sh bz wx chromatid is infrequently produced) and one with C ds sh bz wx. These plants could be Ac Ac or ac ac. The exact genic constitutions of chromosomes 9 in the plants in sub-cultures K and L could not be projected in advance other than to anticipate the presence of the duplication chromosome 9 resulting from a crossover in regions 2 to 5 in the mother plant (or rarely in region 1). Tests of the genic and chromosomal constitutions of these plants will now be given.

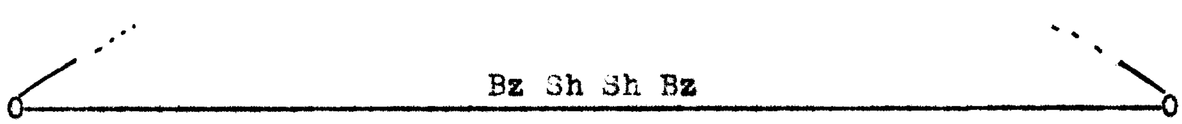
(c) Sub-culture F

By appropriate crosses of plants in sub-cultures F to L, the genic constitutions of the two chromosomes 9 in each tested plant was determined. Plant 4628F-1, known to have two morphologically normal chromosomes 9 because it was examined cytologically, was crossed to two C ds sh bz wx ds ac female plants. The types of kernels appearing on the two resulting ears are given in table 9. This plant was obviously Ac Ac (allelic positions) in constitution. The supplement to table 9 indicates the types of chromatids that plant 4628F-1 would produce on the basis of the given constitution. The observed ratios of the various classes of kernels on these ears confirms the projected constitution of this plant. The plant had a normal chromosome 9 with I Ds^{1} Sh Bz wx and a normal chromosome 9 with C ds sh bz wx. The Ds locus is present just to the right of I. It should be noted that crossing-over between I and Sh is not affected by the presence of this Ds locus (4.9% crossing-over).

With the same aleurone genes in chromosome 9, the variegation pattern produced by a Ds locus in this new position is strikingly different from that produced by a Ds locus in its standard location. In this new position, a Ds mutation will give an acentric fragment carrying I and a dicentric chromatid with Sh Bz wx, as shown in the following diagram:



The dicentric chromatid produced by a Ds mutation at this locus will undergo the breakage-fusion-bridge cycle beginning in the anaphase following the Ds mutation. In this first anaphase, the genes Sh and Bz will be located close to the middle of the bridge:



Because the bridge may be broken at any position between the two centromeres, it can be anticipated that some of the breaks in this

Table 9

Cross of 4628F-1

$\frac{\text{I } Ds' \text{ Sh Bz wx}}{\text{C ds sh bz wx}}$

C sh bz ds ac♀ x $\frac{\text{I } \overset{1}{\downarrow} Ds \overset{2}{\downarrow} Sh \overset{3}{\downarrow} Bz}{\text{C ds sh bz}}$ Ac Ac ♂ 4628F-1

Kernel type	Cross-over region	4368C-4 x 4628F-1	4363-14 x 4628F-1	Totals
I-C Bz-C bz, Sh-sh	non-c.o.	181	89	270
C sh bz	non-c.o. Regions 1&2	153	83	236
I sh	Region 1 Regions 1&3	1	1	2
C Bz-C bz, Sh-sh	Region 1	0	1	1
I bz-C bz, sh	Region 2	8	4	12
C Sh Bz	Region 2	6	6	12
I bz-C bz; Sh-sh	Region 3	10	6	16
C sh Bz	Region 3	2	3	5
I Sh	Regions 1&2	9	0	9*
C bz; Sh-sh	Regions 1&3	1	0	1
I Bz-C bz; sh	Regions 2&3	0	0	0
C Sh bz	Regions 2&3	0	0	0
Totals		371	193	564

* This class is not accurate for showing cross-over regions. It includes (1) losses of Ac and (2) loss, transposition or changes in state of Ds^1.

Supplement to Table 9

Chromatids produced by plant 4628F-1

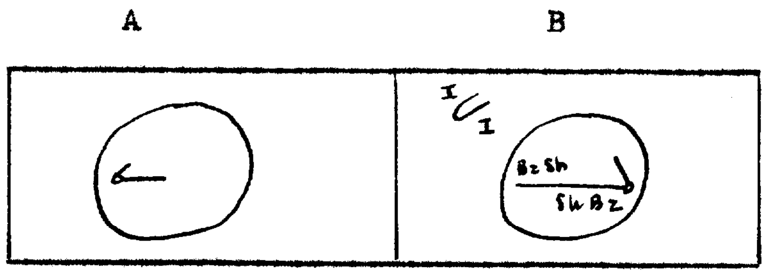
1 2 3

I Ds Sh Bz

C ds sh bz

	Chromatid constitutions	Appearance of kernel in table 9
Non-crossovers	I Ds Sh Bz	I-C Bz-C bz, Sh-sh
	C ds sh bz	C sh bz
Cross-overs	I ds sh bz	I sh
Region 1	C Ds Sh Bz	C Bz-C bz, Sh-sh
Cross-overs	I Ds sh bz	I bz-C bz, sh
Region 2	C ds Sh Bz	C Sh Bz
Cross-overs	I Ds Sh bz	I bz-C bz; Sh-sh
Region 3	C ds sh Bz	C sh Bz
Double cross-overs	I ds Sh Bz	I Sh
Regions 1 and 2	C Ds sh bz	C sh bz
Regions 1 and 3	I ds sh Bz	I sh
	C Ds Sh bz	C bz, Sh-sh
Regions 2 and 3	I Ds sh Bz	I Bz-C bz, sh
	C ds Sh bz	C Sh bz

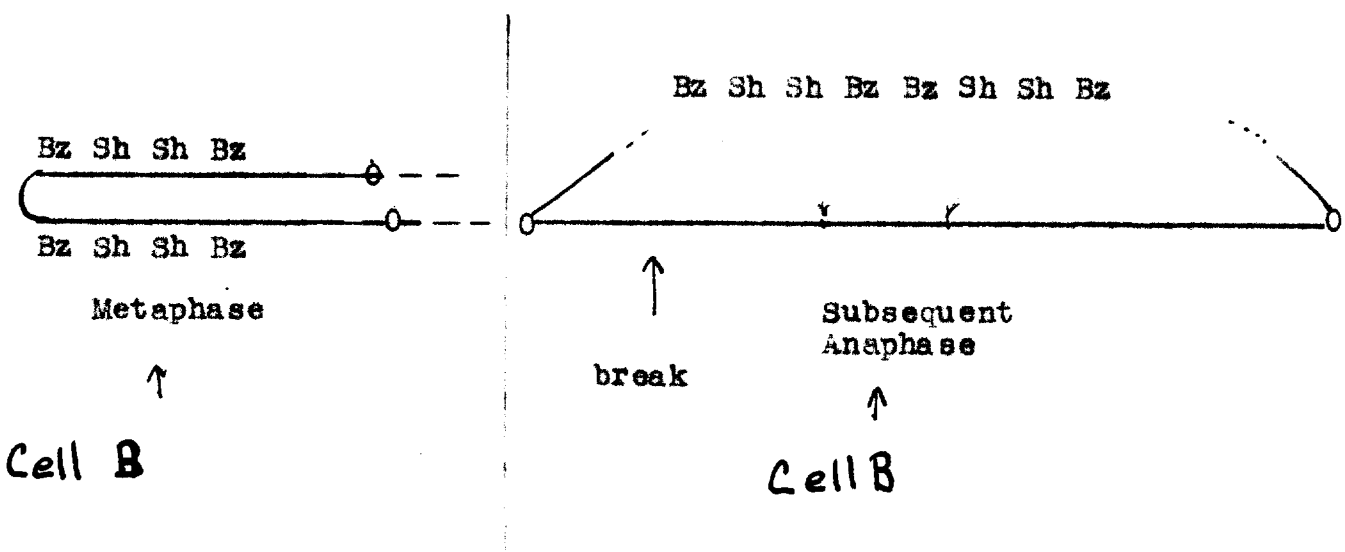
division will occur to one side of this Bz Sh Sh Bz segment instead of within this segment. This would give rise to two daughter cells, one containing no Sh or Bz locus and one containing two Sh and two Bz loci. The I locus, carried by the acentric fragment, would be lost to both daughter cells:



No I, Sh or Bz loci

No I locus; two Sh; two Bz loci

These two sister cells should give rise to two adjacent (twin) sectors in the endosperm, one having a C bz phenotype and one having a C Bz phenotype in which C bz areas appear. These C bz areas would arise from the continuation of the breakage-fusion-bridge cycle in cell B that was initiated by the original Ds mutation:



Twin sectors of the type diagrammed above were present in all of the variegated kernels in table 9.that received an I Ds Sh Bz wx chromosome from the male parent. This variegation pattern is very striking and is strong evidence for the presence of a Ds locus just to the right of the I locus. That this location is correct, is obvious from the genic constitutions and accompanying variegation or lack of variagation in the crossover chromatids recovered from plant 4628F-1 (table 9).

Plant 4628F-2 had the same chromosomal and genic constitution as plant 4628F-1 with respect to the aleurone genes carried by the two chromosomes 9. When crossed to C sh bz wx ds ac female plants, no variegated kernels appeared (table 10-a). When crossed to a C sh bz wx ds,Ac ac plant, again no regular variegated kernels appeared (Table 10-b). From this cross, it may be concluded that plant 4628F-2 has the constitution I Sh Bz wx / C sh bz wx. It does not carry a Ds locus that is regularly producing a dicentric chromatid carrying genes in the short arm of chromosome 9. That a Ds locus may be present was suggested by the presence of a small amount of variegation appearing on a few of the kernels represented in table 10-b. This plant may have a newly transposed Ds locus or a Ds locus with a changed state giving few if any dicentric chromatids (extreme few-late Ds?). These possibilities will be tested this summer.

(d). <u>Sub-culture G</u>

Plants 4628 G-1, G-2 and G-3 proved to be similar in the chromosomal and genic constitutions of their chromosomes 9. All had a normal chromosome 9 with I Ds Sh Bz wx and a normal chromosome 9 with C ds sh bz wx. All were Ac ac. Table 11-a shows the types of kernels

Table 10-a

C sh bz wx ds ac ♀ x 4628F-2 $\dfrac{\text{I "Ds"}^{*}\text{ Sh Bz}}{\text{C ds sh bz}}$ ♂

Cross	Kernel types				
	I Sh	I sh	C Sh Bz	C sh Bz	C sh bz
4363-2 x 4628F-2	115	6	6	3	84
4462C-4 x 4628F-2	219	15	23	6	226
4462C-9 x 4628F-2	210	14	12	13	213
Totals	544	35	41	22	523

Total kernels: 1165

* See text

Table 10-b

C sh bz ds, Ac ac ♀ x 4688F-2 ♂

	Kernel types			
I Sh	I sh c.o. region 1	C Sh Bz c.o. Region 1	C sh Bz c.o. region 2	C sh bz
146	8	11	4	173

Total kernels: 342

appearing on the ears following the cross of these plants to C sh bz wx ds ac female plants. The results obtained are similar to those recorded in table 9 with respect to the types and frequencies of the chromatids that were produced by the heterozygous parents. Because of the Ac ac constitution of these plants, the presence of Ds may be detected in only half of the kernels that received a chromosome 9 carrying a Ds locus. The variegation patterns in the kernels having both Ds and Ac are the same as those appearing on the ears from similar crosses involving plant 4628F-1 (see page 13).

In table 11-b, the types of kernels are given that resulted from the cross of two of the 3 plants in sub-culture G to c sh Bz wx ds ac female plants. Crossing over is normal in frequency in the I to Sh segment, as indicated in both tables 11-a and 11-b (5.5% and 3.9%, respectively). Among the 1243 kernels in table 11-b there were only 2 that were C to c variegated. Both kernels carried Sh in the C Ds chromosome. In table 11-a, there were only 3 C Bz - C bz kernels on the ear among the 1461 kernels. All three carried Sh in the C Ds chromosome. The chromatids carrying C Ds Sh Bz wx should represent the cross overs that occurred in region 1,--between I and Ds. These 5 cases in tables 11-a and 11-b, represent approximately one-fourth of the crossovers in this region that are expected to be present on these ears. If it may be assumed that there are 20 cross-overs in the region between I and Ds among the 2704 kernels on these ears, the cross over percent in this region is approximately 0.74. The C variegated kernels on these ears will be planted this summer and the individuals arising from these kernels will be tested for the presence of a Ds locus just to the right of the C locus in order to be

Table 11-a

C sh wx ds ac ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂

(handwritten "bz" inserted above "wx" with a caret)

Kernel type	4367B-2 x 4628G-1	4360A-2 x 4628G-2	4363-1 x 4628G-2	4363-14 x 4628G-2	4462C-8 x 4628G-3	4684-3 x 4628G-3	Totals
I-C Bz-C bz, Sh	107	19	18	38	108	61	351
I Sh	109	26	25	32	106	48	346
C sh bz	202	45	25	53	219	97	641
I sh	7	3	2	4	5	1	22
C Bz-C bz,Sh	0	1	0	1 *	0	1 **	3
C Sh Bz	8	2	2	0	17	6	35
I bz-C bz, sh	8	1	2	2	12	1	26
I bz-C bz, Sh	3	0	1	0	6	2	12
C sh Bz	10	2	0	4	6	3	25
C bz; Sh-sh	0	0	0	0	0	0	0
C Sh bz	0	0	0	0	0	0	0
I-C Bz-C bz, sh	0	0	0	0	0	0	0
Totals	454	99	75	134	479	220	1461

Summary: 757 I : 704 C Crossing-over I to Sh = 5.5%

* [illegible] 4884 [illegible]

** " 4885. The kernel had areas only of C Bz - C bz, no Ds present. Variegation due to a spontaneous "[illegible]" during development of kernel

Supplement to table 11-a

C sh bz ds ac ♀ x $\dfrac{\text{I Ds Sh Bz}}{\text{C ds sh bz}}$ Ac ac ♂

					Frequencies of critical classes
Non-crossover chromatids	I Ds Sh Bz	Ac	=	I-C Bz-C bz, Sh-sh	351
		ac	=	I Sh	
	C ds sh bz	Ac and ac	=	C sh bz	
Crossovers Region 1	I ds sh bz	Ac and ac	=	I sh	
	C Ds Sh Bz	Ac	=	C Bz-C bz, Sh-sh	3
		ac	=	C Sh Bz	
Crossovers Region 2	I Ds sh bz	Ac	=	I bz-C bz, sh	26
		ac	=	I sh	
	C ds Sh Bz	Ac and ac	=	C Sh Bz	
Crossovers Region 3	I Ds Sh bz	Ac	=	I bz-C bz, Sh-sh	12
		ac	=	I Sh	
	C ds sh Bz	Ac and ac	=	C sh Bz	25
Double crossovers Regions 1 and 2	I ds Sh Bz	Ac and ac	=	I Sh	
	C Ds sh bz	Ac and ac	=	C sh bz	
Regions 1 and 3	I ds sh Bz	Ac and ac	=	I sh	
	C Ds Sh bz	Ac	=	C bz, Sh-sh	0
		ac	=	C Sh bz	0
Regions 2 and 3	I Ds sh Bz	Ac	=	I Bz-C bz, sh	0
		ac	=	I sh	
	C ds Sh bz	Ac and ac	=	C Sh bz	0

Table 11-b

c sh Bz ds ac ♀ x $\frac{\text{I Ds Sh}}{\text{C ds sh}}$ Ac ac ♂

4628G-1 and G-3

Kernel type	Cross-over regions	4353-2 x 4628G-1	4347-22 x 4628G-3	4353-14 x 4628G-3	4347-43 x 4628G-3	Totals
I Sh	Non c.o. Ac and ac Regions 1 & 2 Ac and ac	195	167	147	74	583
C sh	Non c.o. Ac and ac Regions 1 & 2 ac	197	157	169	88	611
I sh	Region 1 Ac and ac " 2 Ac and ac	11	6	11	4	32
C-c Sh	Region 1 Ac	1 *	1 **	0	0	2
C Sh	Region 1 ac Region 2 Ac and ac	2	7	2	4	15
C-c sh	Regions 1 and 2 Ac	0	0	0	0	0
	Totals	406	338	329	170	1243

* see summer 1949, culture 4882 = C Ds Sh ac

** see summer 1949, culture 4876 = no germination sure that no event other than Ds mutations were responsible for the appearance of the C Bz - C bz or C to c variegation in these kernels. The presence of the Sh locus in all five of these kernels strongly supports a C Ds Sh constitution that arose from a crossover in region 1.

(e). Sub-culture H

Tests of the genic constitutions of the two normal chromosomes 9 in each of the two plants in sub-culture H are not extensive. Plant 4628H-1 was crossed to a C sh bz wx ds, Ac ac female plant. The types of kernels appearing on the resulting ear are given in table 12-a. The genic constitutions of the chromosomes 9 in this plant are the same as those in plants F-1, G-1, G-2 and G-3 (I Ds^1 Sh Bz wx / C ds sh bz wx). Plant 4628H-1 should be Ac ac from the appearance of the kernel from which it arose. The kernels of the ear should be Ac Ac Ac, Ac Ac ac, Ac ac ac or ac ac ac. The variegation pattern on the kernels coming from this cross indicate the presence of these various Ac constitutions. In the Ac Ac ac kernels, the presence of an I Ds Sh Bz chromosome was detected by the numerous speckles of C Bz phenotype. In the Ac Ac ac kernels carrying an I Ds Sh bz or I Ds sh bz chromosome, the speckles of C bz could not be detected. The color contrast is too faint. In the Ac ac ac kernels, however, the C bz color may be seen for many large sectors of this phenotype are present. Table 12-a does not give satisfactory data, therefore, on the presence or absence of Ds in some of the kernels having an I Ds sh bz wx or an I Ds Sh bz wx chromosome. The variegation pattern in the Ac ac ac kernels that received an I Ds Sh Bz chromosome is like that described for similar crosses involving plant 4628F-1. Crossing over between I and Sh is normal in frequency (3.6%).

Table 12-a

C sh bz wx ds, Ac ac ♀ x $\frac{\text{I Ds Sh Bz wx}}{\text{C ds sh bz wx}}$ Ac ac ♂

4462C-7 4628H-1

Kernel type	Number of kernels
I Sh (not obviously variegated)	104
I-C Bz-C bz, Sh-sh	172
I sh (not obviously variegated)	10*
I bz-C bz, sh	2
I bz-C bz, Sh-sh	1
C Sh Bz (not obviously variegated)	6
C sh Bz	9
C Sh bz	1
C sh bz	220
Total	525

* I Ds sh bz, Ac Ac ac constitutions not distinguishable because color in C bz specks is not deep enough.

Table 12-b

Re $\dfrac{\text{c Sh Bz wx ds}}{\text{C sh bz wx ds}}$ ac ac ♀ x $\dfrac{\text{I Ds Sh Bz wx}}{\text{C ds sh bz wx}}$ Ac ac ♂

4365-3 4628H-1

Kernel type	Number of kernels
I Sh	139
I-C Bz-C bz, Sh-sh	68
I sh	4
I bz-C bz, Sh-sh	3
C sh Bz	5
C Bz-C bz, Sh-sh	2 *
C sh bz	103
C Sh Bz	127
C-c Sh Bz	2 * *

* see culture 4990 C, summer 1949 { 1 = C Ds Sh Bz wx; 1 = I Ds Sh Bz wx = early loss of I, leaving Sh Bz in clrs.

* * see culture 4890 D, summer 1949 = both C Ds Sh Bz wx

Plant 4628H-1 was also crossed to an ac ac female plant having a rearranged chromosome 9 with c Sh Bz wx ds and a normal chromosome 9 with C sh bz wx ds. The types of kernels appearing on this ear are given in table 12-b. These types and their relative frequencies are expected from the given chromosomes 9 and Ac constitutions of plant H-1.

The constitution of plant 4628H-2 was not examined by outcrossing to appropriate tester plants. Its constitution is very probably the same as that of H-1. This was suggested by a cross of this plant to one having a cm-1 locus. ~~The~~ numerous types of kernels were ~~numerous~~ present on the resulting ear and will not be described.

(f). Sub-culture I.

The two plants in sub-culture I (those arising from I sh wx kernels, table 3) were crossed to a series of tester plants. Plant 4628I-1 had two normal chromosomes 9. Both chromosomes 9 carried C sh bz wx. This constitution suggests that heterofertilization had occurred or that the kernel from which this plant arose had been misclassified. It may have been a C sh bz wx kernel with poor C bz color development. The C bz color in the kernels on the ear of plant 4306 and on the ears in crosses of the plants in culture 4628 is, however, very well developed. Classification for C bz phenotypes are distinct. Plant 4628I-2 had two normal chromosomes 9, one carrying I Ds sh bz wx and one carrying C ds sh bz wx. This plant was ac ac. When crossed to a C sh bz wx ds ac female plant, no variegated kernels appeared on the ear (table 13-a). When crossed to a Ds c sh bz wx ~~C Sh Bz~~ / C Sh Bz wx, Ac Ac plant, 91 of the 94 I Sh wx kernels ~~receiving an I chromosome~~ were I-C variegated (table 13-b). When crossed to a C Bz / C bz, Ac ac female plant, 109 of the 198 I carrying kernels were either I - C Bz or I bz - C bz

Table 13-a

$$C\ sh\ bz\ wx\ ds\ ac\ ♀\ \times\ \frac{I\ Ds\ sh\ bz\ wx}{C\ ds\ sh\ bz\ wx}\ ac\ ac\ ♂$$

4628I-2

Cross	I sh non-variegated	C sh non-variegated
4363-5 x 4628I-2	145	120
44620-3 x " "		
Totals		

Table 13-b

C Bz / C bz, Ac ac ♀ x 4628I-2 ♂

Cross	I kernels		C kernels
	I, non-variegated	I-C variegated	
4372-3 x 4628I-2	99	109	235

Table 13-c

Re $\bullet \dfrac{c\ sh\ \overset{Bz}{}Wx}{C\ Sh\ \underset{Bz}{}wx}$ Ac Ac ♀ x 4628I-2 ♂ I Ds sh bz wx / C ds sh bz wx ac ac

Cross	I kernels, Sh wx		C sh Wx	C sh wx	I sh Wx
	Colorless, Sh wx non-variegated	I-C variegated			
4380A-3 x 4628I-2	1	39	44	66	70
4380A-8 x " "	2	53	70	59	51
Totals	3	91	114	125	121

Odds: 1 C sh wx; 1 I sh wx; 1 possible C-c sh Wx *

* see culture 4891 summer 1948
No Ds in this kernel.

Table 13-d

c / c, Ac Ac ♀ x 4628 I-2 ♂

Cross	I kernels	C kernels	
		C-c variegated	C, non-variegated
4354-5 x 4628I-2	42	1	70
4354-6 x " "	108	0	100
Totals	150	1	170

variegated (table 13-b). This plant was also crossed to a c / c, Ac Ac female plant. Among the 171 C kernels on the ear, only 1 appeared to be C - c variegated (table 13-d). This latter kernel showed only very late Ds mutations--a uniform pattern of c specks--characteristic of Ds mutational responses to two doses of this particular Ac locus. The evidence from all of the crosses indicate the correctness of the given constitution of plant 4628I-2.

The constitutions of the plants in sub-cultures F, G, H and I, that arose from the I carrying class of crossover chromatids on the self-pollinated ear of plant 4306 (table 3), are those expected from the given constitution of this parent plant. A summary review of the constitutions of these plants is given in table 18. The reciprocal crossover classes, those carrying the duplication and having a C locus instead of an I locus, should be represented in sub-cultures K and L. The genetic analysis of these latter plants has given the final evidence that is required to substantiate the projected nature of the event that brought about the transposition of the Ds locus.

(g). Sub-culture K

The constitution of plant 4628K-1 (Duplication chromosome 9 with C ds sh bz Wx Wx Bz Sh Ds^2 / normal chromosome 9 with C ds sh bz wx ds, Ac Ac) was determined by the types of kernels appearing on the ear when this plant was crossed to a C sh bz ds ac female plant (table 14-a). All but three of the C Sh Bz Wx kernels were C Bz - C bz, Sh-sh, Wx-wx variegated. In these kernels, there were no extensive wx sectors regularly appearing in the C Bz areas. Also, all bz areas were wx and where sh could be recognized, all were sh. This type of variegation would indicate that only one Ds locus was present and that it must be located to the right of the duplicated segment~~s~~.

Table 14-a

C sh bz wx ds ac ♀ x $\frac{\text{C ds sh bz Wx Wx Bz Sh Ds}^2}{\text{C ds sh bz wx ds}}$ Ac Ac ♂

4462C-3 4628K-1

♂: Duplication chromosome 9			♂: Normal chromosome 9	
C Sh Bz Wx not obviously variegated	C Bz-C bz, Sh-sh Wx-wx	C Sh* bz wx	C sh bz Wx	C sh bz wx
3	134	2	8+	323**

* Sh is possibly, not positive = sh 10/20/49
\+ 1 of these is very dark in bz color
** 6 of these have very dark bz color

see [illegible] 4892F

	C ds sh bz Wx Wx Bz Sh Ds^2
Duplication chromosome	C ds sh bz Wx Wx Bz Sh Ds^2
Normal chromosome	C ds sh bz wx

Cross-overs: Duplication: C ds sh bz wx Wx Bz Sh Ds^2

Normal chromosome: C ds sh bz Wx ds

Normal chromosome class (minus 2 uncertain C Sh bz wx kernels): 331
see note above

Crossovers : 2.4%

Table 14-b

Re ● c Sh Bz wx ds / C ds sh bz wx ds   ac ac ♀ x 4628K-1 ♂

4365-1

♀ chromosome: C sh bz wx ds				♀ chromosome: c Sh Bz wx ds		
♂ Duplication chromosome 9		♂ normal chromosome 9		♂ Dupl.chr.9	♂ nor. chr.9	Odds
C Sh Bz Wx Non-variegated	C Bz-C bz, Sh-sh, Wx-wx	C sh bz Wx	C sh bz wx	C-c, Sh Bz Wx-wx	C Sh Bz wx	
5	56	1	150	65	122	2 broken C wx ♀ / C Sh Bz Wx Ds ♂ *

* To be expected from crossing over involving Re chromosome 9 and normal chromosome 9 in ♀ parent

←— Eight of the C sh bz kernels were Wx. None of these, however, showed any Wx to wx variegation. In order to rapidly visualize the types and frequencies of chromosomes 9 constitutions that the gametes of this plant could have, a diagram of the usual synaptic association of the two chromosomes 9 in this plant and the resulting types of cross-over chromatids, is included with table 14-a. It may be seen from this diagram that the 8 C sh bz Wx kernels could arise from crossing over in the region of the arrow--between the distal Wx locus and the point that marks the beginning of the proximal duplicated segment. These chromosomes--carrying C sh bz Wx--should be normal in morphology and should have no Ds locus. Therefore, no Wx - wx variegation should appear in the kernels receiving such a chromosome. As stated above, no Wx - wx variegation appeared in the C sh bz Wx kernels.

This same plant was crossed to an ac ac female plant having the rearranged chromosome 9 with c Sh Bz wx ds and a normal chromosome 9 with C sh bz wx ds (table 14-b). In this cross, the 65 C - c, Sh Bz Wx - wx kernels arose from fusion of a female nucleus carrying the c Sh Bz wx chromosome with a male nucleus carrying the Duplication chromosome. In the resulting variegated kernels, all the c areas were wx. No extensive wx sectors regularly appeared in the C areas. Again this shows that the Ds locus in the Duplication chromosome 9 of the male parent must be to the right of the Wx loci.

With regard to chromosomes 9, plant 4628K-2 had the same genic and chromosomal constitution as plant K-1. It was, however, ac ac. When crossed to C sh bz wx ds ac female plants (table 15-a) or to c sh Bz wx ds ac female plants (table 15-b), no variegated kernels appeared. There were only three types of kernels on the ear in each of these two crosses. On the basis of the given constitution of

Table 15-a

C sh bz wx ds ac ♀ x $\frac{\text{C ds sh bz Wx Wx Bz Sh Ds (Dup) ac}}{\text{C ds sh bz wx (normal)}}$ ac ♂

4628K-2

Cross	♂ Duplication chromosome 9	♂ normal chromosome 9	
	C Sh Bz Wx non-variegated	C sh bz Wx	C sh bz wx
4361-11 x 4628K-2	124	4	132

Crossovers in sh class: 3-%

Table 15-b

c sh Bz wx ds ac ♀ x 4628K-2

Cross	Duplication chromosome 9	Normal chromosome 9	
	C Sh Bz Wx	C sh Bz Wx	C sh Bz wx
4347-6 x 4628K-2	167	3	214

Crossovers in sh class: 1.4%

Table 15-c

C sh bz wx ds, Ac ac ♀ x 4628K-2 ♂

Cross	Duplication chromosome 9		Normal chromosome 9	
	C Sh Bz Wx non-variegated	C Bz-C bz, Sh-sh, Wx-wx	C sh bz Wx Non-variegated	C sh bz wx
4462C-2 x 4628K-2	70	63	13	213

Crossovers in sh class: 5.7%

plant 4628K-2, only three types of kernels are to be expected. The C sh Wx kernels in both tables, should have a normal chromosome 9 carrying C sh bz Wx that arose from a crossover in the region between the distal Wx locus and the position that marks the beginning of the proximal duplicated segment. This crossover distance is 3% and 1.4% of the C sh kernels in tables 15-a and 15-b, respectively, and is similar to that observed for the same region in plant 4628K-1.

When plant 4628K-2 was crossed to a C sh bz wx ds, Ac ac female plant (table 15-c) approximately half of the kernels receiving a chromosome 9 carrying C Sh Bz Wx were C Bz - C bz, Sh - sh, Wx - wx variegated. There were 13 C sh bz Wx kernels (5.7% of the C sh bz class) and again none of these 13 kernels showed any Wx to wx variegation. As explained above, variegation is not expected in these kernels.

Plant 4628K-2 was crossed to an Ac ac plant carrying c Sh Bz Wx Ds in a normal chromosome 9 and c sh Bz wx ds in a rearranged chromosome 9 (table 15-d). The appearance of the 79 C - c variegated kernels in the Sh Wx class is expected from the given constitution of this plant. (Segregation of these 79 C-c kernels into the 2 classes, Sh Wx and Sh-sh, Wx-wx, has not been indicated in the table.) These C-c kernels have Ac Ac ac constitution. The Ds mutations occur late in development, as might be expected.

(h). <u>Sub-culture L</u>

Plant 4628L-1, which arose from a C Sh Bz Wx kernel of table 3, carried C ds Sh Bz Wx Wx Bz Sh Ds^2 in a Duplication chromosome 9 and C ds sh bz wx ds in a normal chromosome 9. Two allelic Ac loci were present (Ac Ac). This plant was crossed to a C sh bz wx ds ac female

Table 15-d

$\frac{\bullet\ c\ sh\ Bz\ wx\ ds}{c\ Sh\ Bz\ Wx\ Ds}$ Ac ac ♀ x 4628K-2 ♂

4435-1

Cross	C Sh Wx non-varie-gated	C-c, Sh(-sh)*, Wx(-wx)	C sh Wx and C sh wx non-varie-gated
4435-1 x 4628K-2	220	79	137

* Some kernels are Sh-sh and Wx-wx variegated; others are not, as expected from constitution of ♀.

plant (table 16-a) and to three c sh Bz wx ds ac female plants (table 16-b). The types of kernels appearing on the ears of these test crosses have made it possible to write the genic constitution of the chromosomes 9 in this plant. Crossing over between the normal chromosome 9 and the Duplication chromosome 9 in the region of the distal duplicated segment occurred frequently and was normal in relative frequencies between the marked loci. The percentages in the marked regions are given in tables 16-a and 16-b. The explanatory supplement accompanying each of these tables will make this evident.

No Wx - wx variegation or extensive wx sectors regularly appeared in the C bz areas of the variegated kernels of table 16-a. All of the C bz areas were wx; none showed Wx - wx variegation. In the cross to the c sh Bz wx ds ac female plants, the Ds mutation in the C Sh Wx kernels resulted in c sh wx sectors. No Wx - wx variegation was present in the C areas and, as stated, all the c areas were wx. Again, large wx sectors were not appearing in the C areas. This type of variegation would be expected if only one Ds locus were present and if its position were to the right of the proximal duplicated segment. It should be noted that none of the C Sh bz wx or C Sh Bz wx kernels in table 16-a was C - c variegated. None should be variegated for these kernels should have a normal chromosome 9 with no Ds locus. These C Sh bz wx and C Sh Bz wx chromosomes arose from a crossover in regions 1 and 2, respectively. It should be noted that no C sh bz Wx kernels were produced. These would appear only if a pollen grain carried a double cross-over chromatid (regions 2 and 3). Such a double cross-over chromatid should appear relatively infrequently. No such chromatid was represented on this ear.

Table 16-a

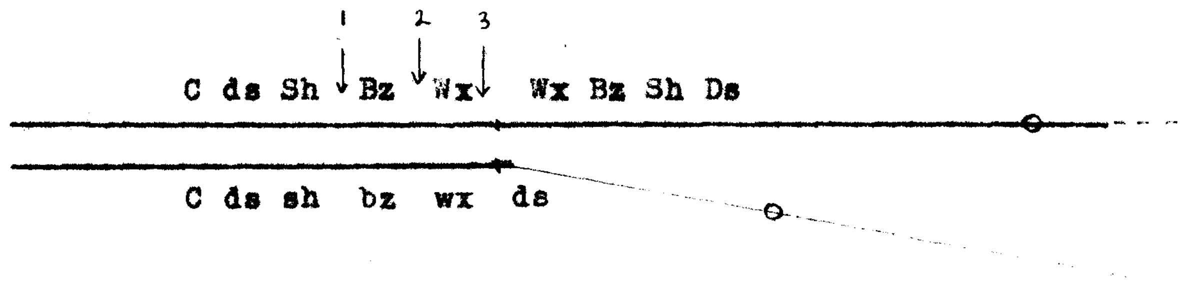
$$\text{C sh bz wx ds ac} ♀ \quad \times \quad \frac{\text{C ds Sh Bz Wx Wx Bz Sh Ds}^2}{\text{C ds sh bz wx ds}}, \quad \text{Ac Ac} ♂$$

4363-3 4628L-1

C Sh Bz Wx	C Bz-C bz, Sh-sh, Wx-wx	C Sh Bz wx non-varie-gated	C Sh bz wx	C sh bz Wx	C sh bz wx
13*	125	74	10	0	128

* Several have a few wx spots.

Supplement to table 16-a



Non-crossovers	C ds Sh Bz Wx Wx Bz Sh Ds	= C Bz-C bz, Sh, Wx-wx	
	C ds sh bz wx ds	= C sh bz wx	128
Region 1	C ds sh Bz Wx Wx Bz Sh Ds	= C Bz-C bz, Sh, Wx-wx	
	C ds Sh bz wx	= C Sh bz wx	10
Region 2	C ds sh bz Wx Wx Bz Sh Ds	= C Bz-C bz, Sh, Wx-wx	
	C ds Sh Bz wx ds	= C Sh Bz wx	74
Region 3	C ds sh bz wx Wx Bz Sh Ds	= C Bz-C bz, Sh, Wx-wx	
	C ds Sh Bz Wx ds	= C Sh Bz Wx	13*

Summary:

Crossing over Region 1 = 4.4%
Region 2 = 32.8%
Region 3 = 5.7%

* Too high; probably includes some <u>No Ds</u> or <u>No Ac</u> gametes due to loss or transposition of Ds or Ac.

Table 16-b

c sh Bz wx ds ac ♀ x 4628L-1 ♂

Cross	C Sh Wx non-varie-gated	C-c, Sh-sh, Wx-wx	C Sh wx	C sh Wx	C sh wx	Odds
4347-4 x 4628L-1	10	129	68	2	117	
4418F-2 x 4628L-1	8	50	36	1	52	1 colorless Wx-wx;Sh *
4418F-2 x 4628L-1	4	39	46	0	73	
Totals	22	218	150	3*	242	

* 1 has defective embryo; probably carries an abnormal chromosome 9.

* See test of this kernel in summer of 1949; culture 4895
Resulted from contamination - Had I Sh Wx Ds Ac / c sh wx ac

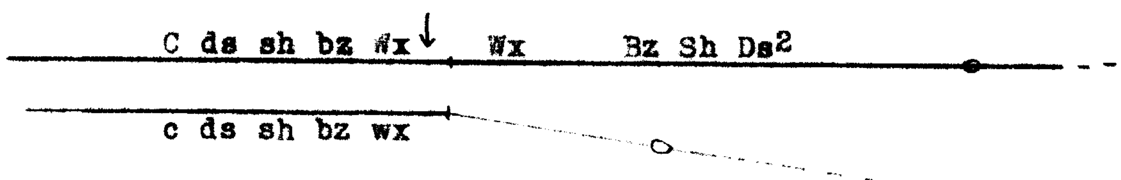
Table 17a

C sh bz wx ds ac ♀ x C ds sh bz Wx Wx Bz Sh Ds^2 Ac ac ♂
C ds sh bz wx ds

4628L-2

Cross	C Sh Bz Wx non-varie-gated (ac ac ac)	C Bz-C bz, Sh-sh, Wx-wx (Ac ac ac)	C sh bz Wx non variegated (Ac ac ac and ac ac ac)	C sh bz wx (Ac ac ac and ac ac ac)
4361-16 x 4628L-2	59	59	11	255
4366-9 x 4628L-2	37	34	11	245
Totals	96	93	22	500

Cross-over region



Cross-overs: C ds sh bz wx Wx Wx Bz Sh Ds^2 Duplication chromosome 9
C ds sh bz Wx ds Normal chromosome 9 = 22

Normal chromosome class : 522
Crossovers : 4.2%

Supplement to table 16-b

c sh Bz wx ds ac ♀ x C ds Sh Bz Wx Wx Bz Sh Ds^2 Ac Ac ♂
C ds sh bz wx

1 2
↓ ↓
<u>C Sh Wx Wx Sh Ds^2</u>
C sh wx ds

Non-crossovers	C Sh Wx Wx Sh Ds^2	= C-c, Sh-sh, Wx-wx	
	C sh wx ds	= C sh wx	242
Region 1	C sh Wx Wx Sh Ds^2	= C-c, Sh-sh, Wx-wx	
	C Sh wx ds	= C Sh wx	150
Region 2	C sh wx Wx Sh Ds^2	= C-c, Sh-sh, Wx-wx	
	C Sh Wx ds	= C Sh Wx	22*
Regions 1 & 2	C Sh wx Wx Sh Ds^2	= C-c, Sh-sh, Wx-wx	
	C sh Wx ds	= C sh Wx	3

* Too high; probably includes <u>No Ds</u>, or <u>No Ac</u> ♂ gametes due to loss or transposition of Ds or Ac.

Summary of crossing over: Region 1 : 36.7%
Region 2 : 6%
Doubles : 0.72% (with no interference would expect 2.27%)

Plant 4628L-2 was similar to plants 4628K-1 and K-2 in the genic and chromosomal constitutions of its chromosomes 9. It was heterozygous for Ac (Ac ac). In crosses to C sh bz wx ds ac female plants, half of the C Sh Bz Wx carrying kernels were C Bz - C bz, Sh - sh, Wx - wx variegated (the Ac ac ac kernels) and half were non-variegated (the ac ac ac kernels), table 17-a. Again, in this cross, a small percentage of the C sh bz kernels were Wx (4.2%) and again, none of these kernels were Wx - wx variegated. The reason for this has been stated previously in the description of similar crosses involving 4628K-1 and K-2.

When plant 4628L-2 was crossed to a c sh Bz wx ds ac female plant, the expected types of kernels appeared, table 17-b. Half of the C Sh Wx kernels were non-variegated and half were C - c, Sh - sh, Wx - wx variegated. In the variegated kernels, all c areas were wx and no large wx sectors were regularly appearing in the C areas. The 13 C sh Wx kernels (3.9% of the sh class) were non-variegated. To repeat, since they carry a normal chromosome 9 with no Ds locus, no variegation should appear.

Plant 4628L-2 was crossed to a c sh Wx, Ac Ac female plant. The kernels resulting from this cross are indicated in table 17-c. No obvious C - c variegation could be observed in approximately half of the C Sh kernels. These are probably the Ac Ac Ac kernels. The kernels showing C - c variegation had a pattern of Ds mutations characteristic of Ac Ac ac constitutions. Again, it may be noted that no C - c variegation was present in the C sh class of kernels. No variegation is expected.

Table 17 b

c sh wx ds ac ♀ x 4628L-2 ♂

Cross	C Sh Wx non-variegated	C-c, Sh-sh, Wx-wx	C sh Wx non-variegated	C sh wx
	Ac	Ac	Ac and ac	Ac and ac
4347-24 x 4628L-2	39	35	13	317

Cross-over region

C ds sh Wx ↓ Wx Sh Ds

C ds sh wx ds

Cross-over:

Duplication chromosome 9

C ds sh wx Wx Sh Ds

Normal chromosome 9

C ds sh Wx = 13

Total kernels = 404

Normal chromosome class : 330

crossovers : 3.9%

Table 17-c

c sh Wx
c' sh Wx   Ac Ac ♀ x 4628L-2 ♂
Ac ac

Cross	Duplication chromosome from ♂		Normal chromosome from ♂
	C Sh Wx Not obviously variegated (Ac Ac Ac)	C-c,Sh-sh, Wx (Ac Ac ac)	C sh Wx non-variegated (Ac Ac Ac and Ac Ac ac)
4355-20 x 4628L-2	65	59*	219

* 58 kernels are speckled with c; late Ds mutation

1 Kernel has an Ac ac ac type of C — c variegation. See Report on Ac inheritance for explanation.

Table 18

Plants arising from various kernels ~~from~~ on self-pollinated ear of plant 4306 (see Table 3).
Chromosomal and genic constitutions of plants of culture 4628; sub-cultures C to L.
Dup. = Duplication chromosome 9. Nor. = Normal chromosome 9

Plant	Chromosome 9 constitution	Activator constitution	Table or page reference	Appearance of kernel from which plant arose
4628C-9	Dup. I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Dup. I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2	Ac Ac	Table 7	I Sh Wx
" D-10	Dup. I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Nor. C ds sh bz wx ds	Ac ac	Table 8	I-C Bz-C bz, Sh-sh, Wx-wx
" D-11	Dup. I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 Nor. C ds sh bz wx ds	Ac ac	Table 8	I-C Bz-C bz, Sh-sh, Wx-wx
" F- 1	Nor. I Ds^1 Sh Bz wx ds Nor. C Ds sh bz wx ds	Ac Ac	Table 9	I Sh wx
" F- 2	Nor. I "ds" Sh Bz wx ds Nor. C ds sh bz wx ds	?	Table 10 (see page 15)	I Sh wx
" G- 1	Nor. I Ds^1 Sh Bz wx ds Nor. C ds sh bz wx ds	Ac ac	Table 11	I-C Bz-C bz, Sh-sh, wx
" G- 2	Nor. I Ds^1 Sh Bz wx ds Nor. C ds Sh Bz wx ds	Ac ac	Table 11	I-C Bz-C bz, Sh-sh, wx
" G- 3	Nor. I Ds^1 Sh Bz wx ds Nor. C ds sh bz wx ds	Ac ac	Table 11	I-C Bz-C bz, Sh-sh, wx

Table 18 continued

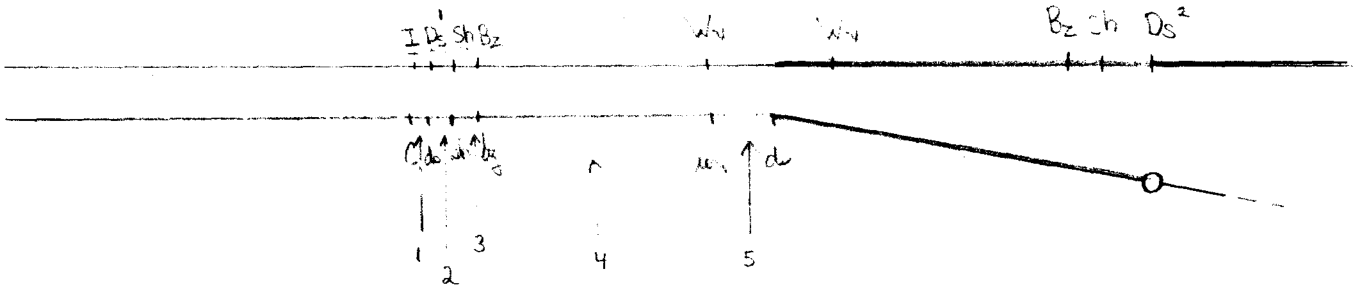
4628H-1	Nor. I Ds^{1} Sh Bz wx Nor. C ds sh bz wx		Ac ac	Table 12	I-C Bz-C bz,Sh-sh,wx
" H-2	(Nor. I Ds^{1} Sh Bz wx Nor. C ds sh bz wx)		Ac ac	See page 18	I-C Bz-C bz,Sh-sh,wx
" I-1	Nor. C sh bz wx Nor. C sh bz wx	Heterofertilization	Not tested	See page 18	I sh wx
" I-2	Nor. I Ds^{1} sh bz wx ds Nor. C ds sh bz wx ds		ac ac	Table 13	I sh wx
" K-1	Dup. C ds sh bz Wx Wx Bz Sh Ds^{2} Nor. C ds sh bz wx ds		Ac Ac	Table 14	C Sh Bz Wx
" K-2	Dup. C ds sh bz Wx Wx Bz Sh Ds^{2} Nor. C ds sh bz wx ds		ac ac	Table 15	C Sh Bz Wx
" L-1	Dup. C ds Sh Bz Wx Wx Bz Sh Ds^{2} Nor. C ds sh bz wx ds		Ac Ac	Table 16	C Bz-C bz,Sh-sh, Wx-wx
" L-2	Dup. C ds sh bz Wx Wx Bz Sh Ds^{2} Nor. C ds sh bz wx ds		Ac ac	Table 17	C Bz-C bz, Sh-sh, Wx-wx

5. Considerationf of the events responsible for the transposition of the Ds locus

The genetic analyses of the plants in culture 4628 has allowed a reconstruction to be made of the genic and morphological constitution of the chromosome 9 in the mother plant (4306). All the tested plants, except 4628C-9, had one normal chromosome 9 carrying C sh bz wx. The constitution of the homologous chromosome 9 in some of the sub-cultures (D, E, G and H) could be anticipated from the type of variegation appearing on the kernels from which these plants arose. The constitutions of plants in sub-cultures F and I could likewise be anticipated within the scope of several simple alternatives. The plants in sub-cultures K and L could have a number of different chromosomal and genic constitutions. To determine the exact constitutions of each plant would require the tests that have been described above.

Figure 1 has been constructed to make this anticipation readily appreciated. Sub-cultures D and E probably received a non-crossover Duplication chromosome 9. Plant 4628I-2 and L-1 received chromosomes arising from a crossover in region 2 in the mother plant. The crossover chromatid in 4628I-2 is the reciprocal of the one present in 4628L-1. Region 4 has the longest unit crossover distance. A crossover in this region would give rise to a morphologically normal chromosome 9 with I Ds^1 Sh Bz wx and a Duplication chromosome 9 with C ds sh bz Wx Wx Bz Sh Ds^2. These two classes of reciprocal crossover chromatids should be the most frequent of all of the crossover classes of chromatids and therefore they should be the most frequent ones recovered in a self-pollination or an outcross. Although the numbers are few, the analysis of the genic constitutions of the chromosomes 9 in the plants in sub-cultures F, G and H and in sub-cultures K and L are in agreement with this expectation.

Figure 1

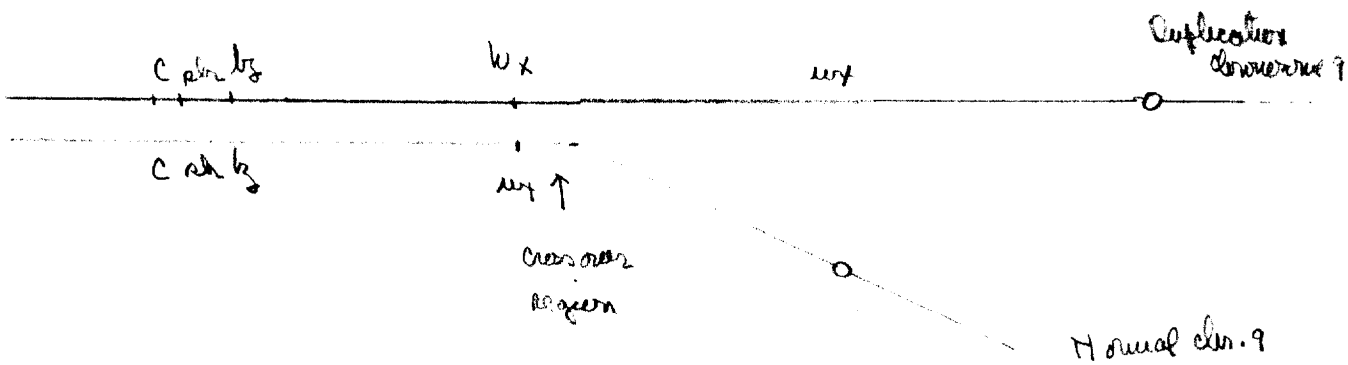


Cross-over chromatids recovered from plant 4306.

Region 2	I Ds^1 sh bz wx; Normal chromosome 9; Plant 4628I-2
	C ds Sh Bz Wx Wx Sh Ds^2; Duplication chromosome 9; Plant 4628L-1
Region 4	I Ds^1 Sh Bz wx; Normal chromosome 9; Plants 4628F-1, G-1, G-2, G-3, H-1, H-2
	I ds sh bz Wx Wx Bz Sh Ds^2; Duplication chromosome 9, Plants 4628K-1, K-2, L-2.

The order of the genes in the proximal segment has been given little consideration in the preceding discussion. It is necessary to indicate, therefore, why this order is required and why the particular marked loci have been placed in this segment. The analysis of the synaptic configurations of a normal chromosome 9 and the Duplication chromosome 9 in the heterozygous plants (pages) and the analyses of the chromosomal and genic constitutions of the recovered crossover chromatids along with their frequencies, has indicated the composition and order of genes in the distal of the two duplicated segments. It is composed of a unit of the normal short arm of chromosome 9 that begins just to the right of the I locus and extends to a locus approximately 4 units to the right of Wx. It is present in the Duplication chromosome 9 in the normal order, as these studies have shown. A Ds locus is present at the junction of this unit with the distal third of the short arm. In other words, the Duplication chromosome 9 has a normal gemic and chromosomal composition from the end of the short arm to a position approximately 4 crossover units beyond Wx with the exception, however, that a Ds locus is present just to the right of the I locus.

The proximal duplicated segment must contain Sh, Bz and Wx. The presence of Wx in this segment is indicated by the crosses of 4628K-1, K-2 and L-2 to C sh bz wx female plants. If no Wx locus were present in this segment of if wx were present, one should obtain some C Sh Bz wx kernels and those having Ac should be C Bz - C bz variegated. They should appear in approximately 4% of the C Sh Bz class for they would be the reciprocals of the C sh bz Wx kernels:



Such kernels would not appear, however, if a Wx locus were carried by the proximal duplicated segment. Such kernels did not appear in the crosses. It could be concluded, therefore, that a Wx locus must be present in this segment.

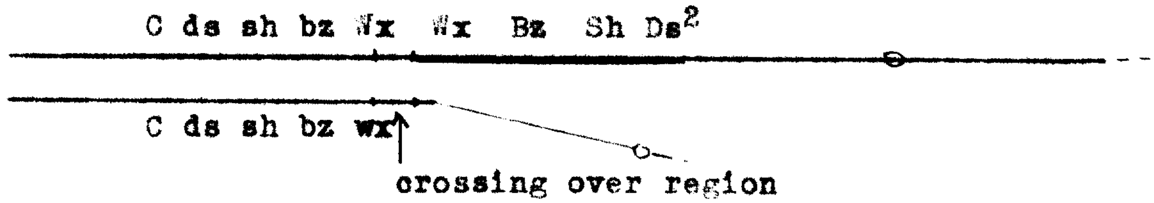
Sh and Bz loci must likewise be present in this segment. The evidence for this is apparent from several considerations. It is most obvious, of course, in the phenotypes produced by the Duplication chromosome 9 in plants 4628K-1, K-2 and L-2. It is the Sh and Bz loci in this proximal segment that accounts for the Sh and Bz phenotypes that appear in the kernels from which each of these plants arose and in the kernels having the Duplication chromosome 9 in crosses of these plants to sh bz plants.

Neither I nor C can be present in the proximal duplicated segment. The absence of a C locus in this segment was considered on page 9 . The absence of an I locus in this segment is apparent from the phenotypes that result from a Ds^1 mutation in an I Ds^1 Sh Bz Wx Wx Sh Bz Ds^2 / C sh bz wx / C sh bz wx, Ac ac ac kernel. A Ds^1 mutation deletes the I locus distal to Ds^1. The resulting phenotype is C. Again, if I were present in this segment a Duplication chromosome 9 with the constitutions shown to be present in sub-cultures 4628 K and L would not be recovered. These chromosomes have no I locus in the proximal segment. Neither an I locus, nor a C locus, therefore, is present in the proximal segment.

All of these considerations point towards the exact composition of the two segments with regard to the loci they carry. The position of breakage that could give rise to such segments is also indicated. The distal segment extends from a position just to the right of I (demarked by the inserted Ds^1 locus) to a position 3 or 4 crossover units to the right of the Wx locus in this segment. Crossing over between a normal chromosome 9 and the Duplication chromosome 9 is normal in kind and relative frequency within this distal segment, as the tables have shown. <u>The crossover unit distance between this distal Wx locus and the junction with the proximal segment in the plants heterozygous for the Duplication chromosome 9 is the same as the crossover unit distance between Wx and Ds-standard in plants with two normal chromosomes 9.</u> A summary of the cross over percentages in this region, that occurred in plants 4628K-1, K-2 and L-2 where it could be determined, is given in table 19. The junction of the two segments is marked by the position that Ds-standard occupies in a normal I Sh Bz Wx Ds chromosome. As shown in tables 1 and 2, the chromosome 9 in plant 4108C-1 that carried I Sh Bz Wx and Ds, was normal in its genetic behavior and had Ds at the standard location. The presence of only two recognizable odd gametes was observed in the crosses of this plant. One of these had the duplication that arose from an aberration occurring within this I Sh Bz Wx Ds chromosome. In this Duplication chromosome 9, the proximal segment has the same genes within it as the distal segment. This indicates that <u>chromosome</u> breakage occurred in a cell of the parent plant (4108C-1) at the Ds locus and also at a position just to the right of the I locus. This was followed by fusions of broken ends that at the same time included a transposition of a Ds locus between two of these ends. Before this event may be reconstructed,

Table 19

Summary ~~of~~ table of percent crossing over between the distal Wx locus and the end of the distal duplicated segment based on the recovered normal chromosomes 9 in crosses of plants 4628K-1, 4628K-2 and 4628L-2



Cross	C sh wx	C sh Wx	Percent crossing over
4362C-3 x 4628K-1	323	8	2.4
4365-1 x 4628K-1	150	1	0.66
4361-11 x 4628K-2	132	4	2.9
4347-6 x 4628K-2	214	3	1.4
4462C-2 x 4628K-2	213	13	5.7
4361-16 x 4628L-2	255	11	4.1
4366-9 x 4628L-2	245	11	4.3
4347-24 x 4628L-2	317	13	3.9
Totals	1849	64	3.3

Total kernels: 1913

it is necessary to inquire into the order of the genes in the proximal segment.

The order of genes in the proximal segment has been determined from two general types of evidence: first, the type of variegation patterns in the kernels having the Duplication chromosome 9 and secondly, the types of chromatids that plants heterozygous for the Duplication have produced. The order could be (1) I Ds^1 Sh Bz Wx Sh Bz Wx Ds^2 or (2) I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2. If (1) were correct, it would be difficult to explain how the large wx areas could arise that frequently appear in the C Bz sectors in the I - C Bz - C bz, Sh - sh, Wx - wx variegated kernels of tables 7-a and 8. If the second of the two genic orders was present, just such wx regions should appear because the breakage-fusion-bridge cycles that are initiated by Ds^1 mutations should often result in deletions of the two Wx loci from some cells while retaining the proximal Bz locus. In the crosses indicated, the resulting cells would be C Bz wx. If order (1) were present, the C Bz sectors that are variegated should have some C bz areas within them that are Wx - wx variegated. As stated earlier, no such C bz areas are present. All of the C bz areas are wx. If order (2) were present, all the C bz areas within the C Bz sectors should be wx for the Wx loci should be lost from some cells by the breakage-fusion-bridge mechanism before the proximal Bz locus is lost. In other words, Bz will not be lost before the Wx loci are lost. In the crosses of plants 4628 K-1, K-2 and L-2 to C sh bz wx plants, no large wx areas appeared in the C Bz sectors of the variegated kernels and none are expected as there is no Ds locus to the left of Ds^2 that, by mutation, could initiate a dicentric chromatid having Bz and Wx in the region between the two centromeres. These several observations, then, strongly support the given inverted order of the genes in the proximal segment.

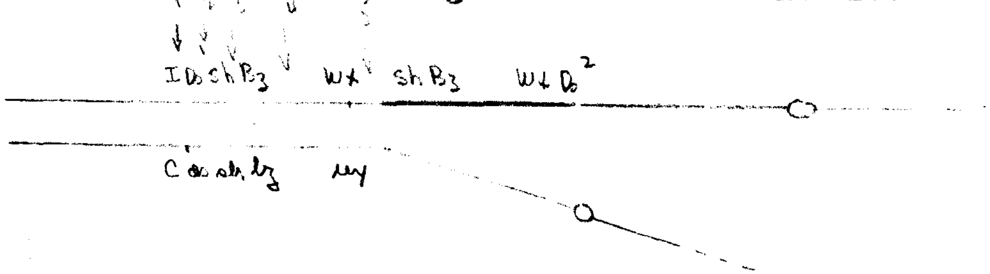
Figure 2

Types of chromatids that should be produced by crossing over with order of genes (1) and (2) in Duplication chromosome 9

Type (1) order

A. Synapsis of distal segment of Duplication chromosome 9 with homologous segment in the normal chromosome 9

Single crossover chromatids



Region 1

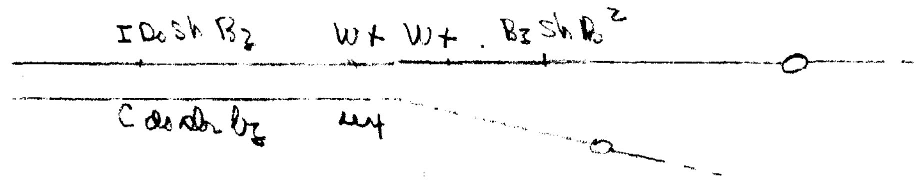
I ds sh bz wx ds — Normal chromosome

C Ds^1 Sh Bz Wx Sh Bz Wx Ds^2 — Duplication chromosome

Type (2) order

A. Synapsis of distal segment of Duplication chromosome 9 with homologous segment in normal chromosome 9

Single crossover chromatids



Region 1

I ds sh bz wx ds — Normal chromosome

C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 — Duplication chromosome

Figure 2 continued

Region 2

I Ds^1 sh bz wx ds — Normal chromosome

C ds Sh Bz Wx Sh Bz Wx Ds^2 — Duplication chromosome

Region 3

I Ds^1 Sh bz wx ds — Normal chromosome

C ds sh Bz Wx Sh Bz Wx Ds^2 — Duplication chromosome

Region 4

I Ds^1 Sh Bz wx ds — Normal chromosome

C ds sh bz Wx Sh Bz Wx Ds^2 — Duplication chromosome

Region 5

I Ds^1 Sh Bz Wx ds — Normal chromosome

C ds sh bz wx Sh Bz Wx Ds^2 — Duplication chromosome

Region 2

I Ds^1 sh bz wx ds — Normal chromosome

C ds Sh Bz Wx Wx Bz Sh Ds^2 — Duplication chromosome

Region 3

I Ds^1 Sh bz wx ds — Normal chromosome

C ds sh Bz Wx Wx Bz Sh Ds^2 — Duplication chromosome

Region 4

I Ds^1 Sh Bz wx ds — Normal chromosome

C ds sh bz Wx Wx Bz Sh Ds^2 — Duplication chromosome

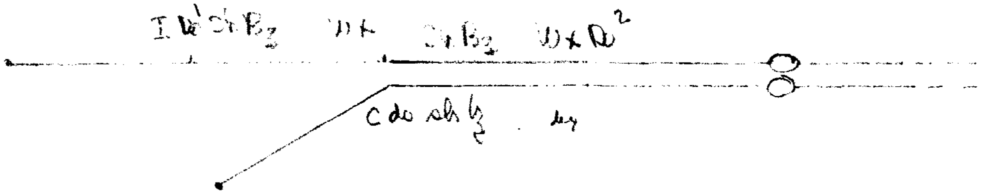
Region 5

I Ds^1 Sh Bz Wx ds — Normal chromosome

C ds sh bz wx Wx Bz Sh Ds^2 — Duplication chromosome

Figure 2 continued

B. Synapsis of proximal segment of Duplication chromosome 9 with homologous segment in Normal chromosome 9



Single crossovers

Region 1

I Ds^1 Sh Bz Wx sh bz wx ds   Duplication chromosome

C ds Sh Bz Wx Ds^2 Normal chromosome

Region 2

I Ds^1 Sh Bz Wx Sh bz wx ds   Duplication chromosome

C ds sh Bz Wx Ds^2 Normal chromosome

Region 3

I Ds^1 Sh Bz Wx Sh Bz wx ds   Duplication chromosome

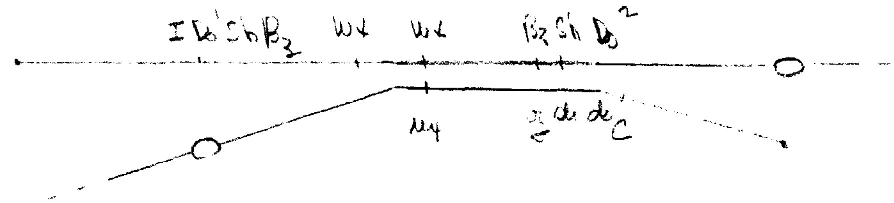
C ds sh bz Wx Ds^2 Normal chromosome

Region 4

I Ds^1 Sh Bz Wx Sh Bz Wx ds   Duplication chromosome

C ds sh bz wx Ds^2 Normal chromosome

B. Segment of proximal segment of Duplication chromosome 9 with homologous segment in Normal chromosome 9



All single crossovers would give a dicentric chromosome and an acentric fragment. The dicentric chromosome would be deficient for the terminal third of the short arm.

That an inverted order is present is again supported by the types of crossover chromatids that could appear if type (1) organization were present but would not appear if type (2) organization had been present in plant 4306 or in plants 4628D-10 and D-11 (table 8). Figure 2 illustrates the types of crossover chromatid that could be anticipated from genic orders (1) and (2) above. Homologous synapsis of the normal chromosome 9 with the distal segment would give phenotypically similar crossover chromatids in the two cases (A, Figure 2). Homologous synapsis of the normal chromosome 9 with the proximal segment, if order (1) were present, could give rise to crossover chromatids having the constitutions shown in B of figure 2. The crossover chromatids that should arise from this association have not appeared. If order (2) were correct, such crossover chromatids would not appear. From this negative evidence, order (2) is again indicated.

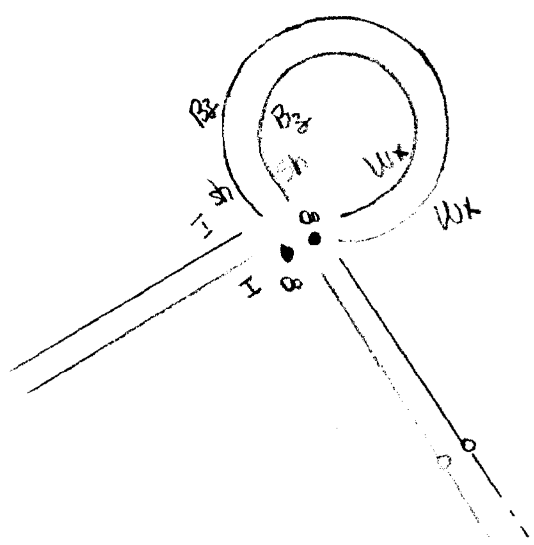
It is possible, now, to reconstruct the events that gave rise to this Duplication chromosome 9 with a transposed Ds locus. Three assumptions regarding these events are required. (1) A Ds mutation occurred at its usual time--late in the development of the sporophytic tissues--in a cell of plant 4108C-1. The chromosome in which this Ds mutation occurred was normal in morphology and carried I Sh Bz Wx and Ds in its standard location. The Ds mutation resulted in breakage of the two sister chromatids at the position of the Ds locus in each chromatid. Evidence that a Ds mutation brings about breaks in sister chromatids at the locus of Ds is well established. This assumption is therefore legitimate. (2) The Ds mutation not only caused breaks to occur at the position of the Ds locus but resulted in the release of a submicroscopic chromatin segment that carries a Ds locus. This released segment carrying Ds has unsaturated broken ends. It could be lost from the chromosome complement if fusion with some other broken ends did not occur. Loss of the Ds locus as a consequence of Ds mutations has been considered in detail elsewhere (see report on c-ml mutations, January, 1949). The manner of this loss may be suggested from cases such as the one being described. (3) At the same time that the events described in (1) and (2) occurred, a spontaneous chromosome break occurred just to the right of the I locus in this chromosome. Both sister chromatids were broken at the same locus. Evidence for frequent spontaneous breaks in maize is good (McClintock, unpublished). This assumption, therefore, is legitimately taken. These three events would give a series of broken ends as shown in A, figure 3. Fusion of broken ends could readily occur to give rise to the configuration shown in B, figure 3. The resulting chromatids are diagrammed in C, figure 3. A Duplication chromosome 9, with an inverted order of genes in the proximal duplicated segment and having a transposed Ds locus just to the right of the I locus is now formed.

On the basis of the depicted mode of origin of the Duplication chromosome 9, it must be assumed that the two Ds loci are daughter Ds loci derived from reduplication of a mother Ds locus. The mutational behavior of the two Ds loci in this chromosome are not alike. More dicentric chromatid-forming mutations occur at Ds^1 than at Ds^2. The states of the two Ds loci definitely differ from one another. This is particularly apparent when these two loci are separated by crossing over and the crossover chromatids isolated. Then, the mutational behavior of Ds^1 may be directly compared with that of Ds^2. Either a change in state occurred in one or both of the Ds loci during one of the events that gave rise to the duplication and the transposition; or a change in state in one or both Ds loci took place subsequent to this event. There is no evidence for any position effect associated with the altered genic associations of the two Ds loci.

Figure 3

A.

Position of chromosome breaks



B.

Fusion of broken ends

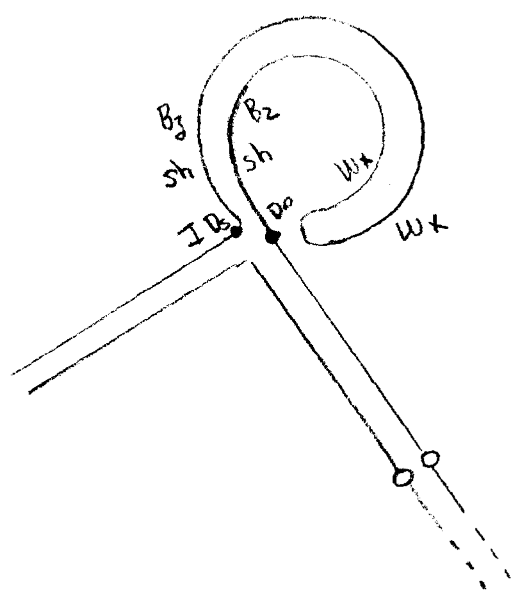
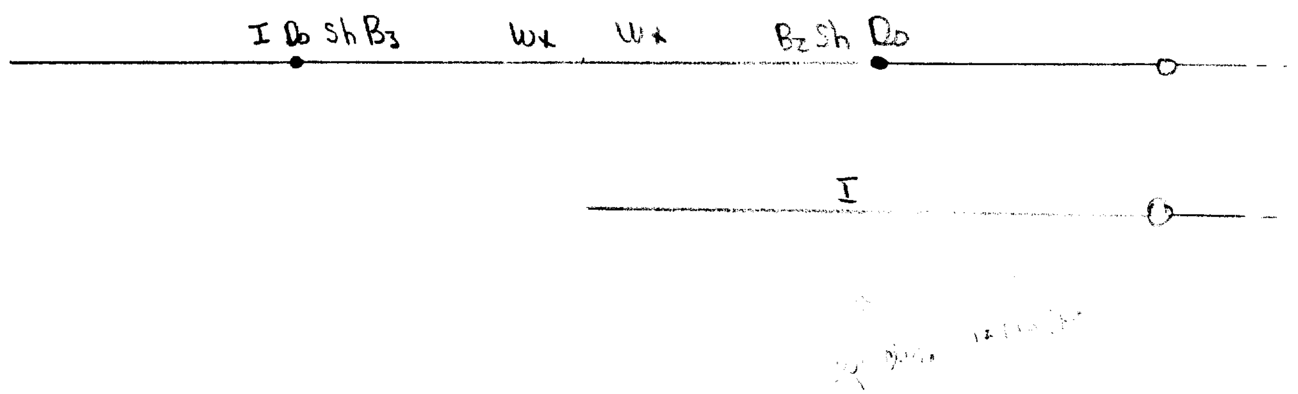


Figure 3 C.

Resulting chromatids



Changes in state of these two separated Ds loci are occurring independently of their positions as a few of the variegated kernels have shown.

Again, it should be emphasized that the transposition of the Ds locus has not introduced any visible alteration in the appearance of the chromosome in the region of the transposition. Neither has its insertion affected the crossing over in the I to Sh region. To refresh this evidence, a summary of this crossing over in the crosses of plants in sub-cultures 4628 F, G and H are given in table 20. These observed crossover percentages are similar to those observed when no Ds locus is present. The inserted segment carrying Ds must be very minute--obviously submicroscopic in size.

The analysis of this case of transposition of Ds has indicated the method for selecting those relatively rare kernels with newly arising transposed Ds loci. In the crosses of I Sh Bz Wx Ds-standard to C sh bz wx ds ac plants, the kernels with aberrant variegation of quite specific types may be selected. It is possible, by this method, to detect those chromosomes having Ds inserted to the left of I, between I and Bz and between Bz and Wx. A number of such kernels have been selected and an analysis of the transposition of the Ds locus is being conducted. Evidence from these other cases should be well advanced by the time the greenhouse crop is collected and certainly by the time the summer crop is harvested.

Table 20

Summary of crossing over between I and Sh in plants 4628F-1, 4628G-1, G-2 and G-3, and plant 4628H-1

$$\frac{\text{Normal chromosome 9} \quad I\ Ds^{1}\ Sh}{\text{Normal chromosome 9} \quad C\ ds\ \ sh}$$

Table reference	Total Number of kernels	Number of cross-over chromatids	Percent Crossing over
Table 9, 4628F-1	564	28	4.9
Table 11-a, 4628b	1461	85	5.5
Table 11-b, 4628b	1243	49	3.9
Table 12, 4628H-1	525	19	3.6
Totals	3793	181	4.7

Appendices to:

Transposition of the Ds locus, April, 1949.

In the previous account the Case I transposition of the Ds locus, April,1949. the origin and behavior of this case of transposition was analysed in considerable detail. Continued examination of this case has resulted in confirmation of the conclusions given in the earlier report. In this supplement, the confirmatory evidence will be given in the form of appendices. The table numbering will follow sequentially from the previous report.

Appendix 1

In the cross given in table 7-c, an Ac ac, C sh bz wx ds female plant was crossed by plant 4628C-9. This latter plant was homozygous for the duplication chromosome 9. Both chromosomes carried I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2. The plant had one Ac locus. A number of kernels appeared on the ear that showed only a few specks of C color (column 1, table 7-c). It could be anticipated that these kernels had 3 Ac loci in their endosperm cells, two contributed by the female parent and one by the male parent. If the Ac loci in both plants were located in allelic positions, the plants arising from these kernels should be Ac Ac. Some of these lightly speckled kernels were selected from the cross of 4462C-11 x 4628C-9 (Table 7-C) and plants grown from them in the summer of 1949 under culture number 4876A. These plants were crossed to: (1) C sh bz wx, ds ac plants (Tables 21-a and 21-b), (2) by C sh bz wx, ds ac plants (Table 22), and (3) to c sh Bz wx, ds ac plants (table 21-c).

In cross (1) above, the types of male gametes, with respect to chromosome 9 morphology and genic constitution, should be the same as those given in the supplement to Table 8. It was hoped, however, that two allelic Ac loci would be present in the tested plants so that a more direct analysis of the chromosome and genic constitutions of the resulting progeny would be available. The four tested plants in Table 21-a had two Ac loci. Unfortunately, however, these two loci did not occupy allelic positions, as the results given in this table indicate. The classes of kernels and their frequencies are those expected if these four tested plants had two non-linked, non-allelic Ac loci. This is shown in the supplement to Table 21-a. It must be concluded, therefore, that the Ac locus in the two parent plants occuppied different positions in the chromosomal complement. In all other respects, however, the results are the same as those given by plants having the same chromosome and genic organizations that were tested in the previous season, Table 8. Therefore, no further description or analysis is required.

In one plant of culture 4876A, the Ac constitution of the main stalk and the tiller differed. This is shown by the frequencies of kernel types obtained when pollen from the main stalk and pollen from the tiller were used in crosses to C sh bz wx, ds ac plants, Table 21-b. The ratios of kernel types obtained when pollen of the main stalk was used indicate that only one Ac locus was present. The pollen from the tiller gave ratios of kernel types that indicate the presence of two non-linked, non-allelic Ac loci. It cannot be decided from these tests whether or not the tiller gained an Ac locus or whether or not the main stalk lost an Ac locus. Either event could account for the observed difference in the two parts of the plant.

Two of the plants entered in Table 21-a were crossed to c sh Bz wx, ds ac plants. The types of kernels appearing on the resulting ears are given in Table 21-c. As the supplement to Table 21-c indicates, the types of kernels and the ratios observed are those expected from the stated constitution of these plants.

In Table 7-c, one aberrant kernel was recorded. This kernel had the phenotype C Sh Bz Wx and was non-variegated. Such a kernel was not expected to appear following the cross given in Table 7-c. A plant was grown from this kernel. It was crossed to a c sh Bz wx, ds ac plant. There were 345 kernels on the resulting ear. 51 were C Sh Wx, non-variegated; 2 were C sh Wx, non-variegated and 292 were C sh wx, non-variegated. When the plant was crossed to a C sh be wx, ds ac plant, the resulting ear showed 27 C Sh Bz Wx non-variegated kernels, 23 C Bz → C bz, Sh, Wx→wx (bz areas wx) kernels, 2 C sh bz Wx non-variegated kernels and 116 C sh bz wx kernels. The plant was likewise self-pollinated. The resulting ear showed 229 C Sh Bz Wx (a number were variegated) one C sh bz Wx and 156 C sh bz wx kernels. If the tested plant had the constitution Duplication C sh bz Wx Wx Bz Sh Ds/C sh bz wx, ac ac, just such ratios following the given cross would be obtained (see Tables 15-b, 15-c and Tables
It is suspected that contamination was responsible for the appearance of the aberrant kernel in Table 7-c, or that the pollen grain that gave rise to this kernel had a deficiency in the distal segment that included the I, Ds, Sh, and Bz loci. Only further tests could distinguish between these two possibilities.

In the April 1949 report, no evidence was presented for the transmission of the duplication chromosome through the egg parent. Plants heterozygous for a normal and a duplication chromosome 9 give reduced transmission frequencies of the duplication chromosome through the pollen. The ratios of ~~the~~ C Sh Bz Wx kernels to ~~the~~ C sh bz Wx and C sh bz wx kernels in the crosses of C sh bz wx by Duplication C sh bz Wx Wx Bz Sh Ds/normal chromosome 9 with C sh bz wx indicate the transmission frequencies through the pollen of the duplication chromosome 9. Compilation of the data from Tables give a ratio of Duplication chromosomes 9 to normal chromosomes 9. Such a reduction in transmission of the duplicated chromosome is likewise evident when plants of the constitution I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2/ C sh bz wx are crossed to C sh bz wx. Because the crossing-over between the distal Wx locus and the proximal segment is low, the frequency of the Wx to the wx class gives the approximate frequencies of transmission of the duplication and the normal chromosome. The combined data from Tables 8, 21-a, 21-b and 21-c show 1694 Wx to 3331 wx kernels. In the reciprocal cross, no such reduction in transmission of the duplication chromosome is expeeted. Four of the plants entered in Table 21 were crossed reciprocally. The results of these reciprocal crosses are given in Table 22. Because of the presence of 4 Ac loci in the endosperms of many of the kernels, it was not possible to make an accurate classification for the presence or absence of Ac in all the kernels. In the table a significant reduction in the Wx class is evident. This is probably not related to a reduction in transmission of the duplication chromosome. Rather, it is related to Ds mutations occurring before meiosis that produced non-female transmissible deficiencies.

Data given in Tables 21 and 22 show that crossing-over between the normal chromosome and the distal duplicated segment in the Duplication chromosome 9 is relatively little affected by the presence of the duplication. This would suggest that synapsis is not seriously disturbed by the presence of the duplication; otherwise, a considerable reduction in crossimg-over between I and Wx would be evident.

Appendix 2

In the summer of 1948, plant 4628K-1 (Tables 14-a and 14-b) having the constitution Dup. C sh bz Wx Wx Bz Sh Ds/C sh bz wx, Ac/Ac, was crossed by plant 4628L-1 (Tables 16-a and 16-b) with the constitution Dup. C Sh Bz Wx Wx Bz Sh Ds/C sh bz wx, Ac Ac. It was hoped that some of the plants arising from the C Sh Bz Wx class of kernels on the resulting ear would be homozygous for the duplication and for Ac. The ear was small and only a few kernels of the desired type were available for testing. Six of these kernels were planted in the summer of 1949 under culture number 4898 but only 4 of them germinated. The constitution of three of these plants were exactly like the female parent plant (4628K-1, Table 14) as the results of reciprocal crosses with C sh bz wx, ds ac plants have shown, Tables 23, 24, and 25.

One of the plants in culture 4898 (4898-2) had the constitution Dup. C sh bz Wx Wx Bz Sh Ds/C Sh bz wx, Ac Ac. The duplication chromosome must have been contributed by the female parent plant whereas the normal chromosome with C Sh bz wx arose from a crossover in region 1 of the male parent plant (see supplement to Table 16-a). Reciprocal crosses of this plant with C sh bz wx, ds ac plants are given in Tables 26-a and 26-b. The cross of this plant to a c sh Bz wx, ds ac plant gave the kernel types listed in Table 26-c. Crossing-over between Sh and Wx in this plant was very high in the microsporocytes but a much lower frequency of recovered crossover chromatids came from the megasporocytes. Such high rates of crossing over in this segment of chromosome 9 have been encountered when two normal chromosomes have been present. A reduced amount of crossing-over in the megasporocytes as compared with the microsporocytes has likewise been observed in numerous tests.

Appendix 3.

In the crosses of C sh bz wx, ds ac plants by Ac ac plants having the Duplication chromosome 9 with I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 and a normal chromosome 9 with C sh bz wx, a number of distinctive kernel types appeared (Table 8). The projected constitutions of these kernels are given in the supplement to Table 8. In order to determine whether the projected constitutions were correct, some of the kernels from the cross-over classes were selected from two of the crosses, 4462C-8 x 4628D-11, and 4363-17 x 4628D-11 (Table 8) and grown in the summer of 1949 under culture numbers 4877 and 4878, respectively. Two plants arising from the I$\rightarrow$C Bz$\rightarrow$C bz, Sh$\rightarrow$sh, wx kernels (4877A), four plants arising from the C Bz$\rightarrow$C bz, Sh$\rightarrow$sh, Wx$\rightarrow$wx kernels (4877C) and the plants arising from two C Sh bz wx kernels (4877E) in cross 4462C-8 x 4628D-11 were tested for their chromosome 9 constitutions. In the cross 4363-17 x 4628 D-11 (Table 8), four plants arising from the C Bz-C bz, Sh-sh, Wx-wx kernels (4878D)were tested for their chromosome 9 constitutions.

Table 29 gives the ratios of kernel types obtained when the two plants arising from the I Bz$\rightarrow$C Bz$\rightarrow$C bz, Sh$\rightarrow$sh, wx kernels were crossed by C sh bz wx, ds ac plants. The results are those anticipated from the given constitions shown in the heading to this table. The plants arising from the C Bz-C bz, Sh-sh, Wx-wx kernels should all have the Duplication chromosome 9 but the genic constitution could be of several types, as the supplement to Table 8 and Figure 2 illustrate. Crossing over in regions 1 to 5 would give the following genic constitutions in the duplication chromosome:

Region 1: Dup. C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2

Region 2: Dup. C Sh Bz Wx Wx Bz Sh Ds^2

Region 3: Dup. C sh Bz Wx Wx Bz Sh Ds^2

Region 4: Dup. C sh bz Wx Wx Bz Sh Ds^2

Region 5: Dup. C sh bz wx Wx Bz Sh Ds^2

Because crossing-over in region 4 is the highest, the majority of the C Bz-C bz, Sh-sh, Wx-wx kernels in the cross shown in Table 8 should give plants with the constitution: Dup. C sh bz Wx Wx Bz Sh Ds/ C sh bz wx, Ac ac. Of the 8 tested plants arising from such kernels,

were definitely Dup. C sh bz wx Wx Bz Sh Ds/C sh bz wx, Ac ac (Table 27, a and b), were Dup. C sh bz Wx(or wx)Wx Bz Sh Ds/ C sh bz wx, Ac ac (Table 27-d). The tests of the latter plants were inadequate for determining the presence or absence of the distal Wx locus. One plant, 4878D-1, had the constitution Dup. C sh Bz Wx Wx Bz Sh Ds/ normal chr. 9 C sh bz wx, Ac ac, as the results of the cross of this plant by a C sh bz wx, ds ac plant indicate (Table 28). The constitution of the duplication chromosome in this plant resulted from a crossover in region 3 of the parent plant.

In cross 4462C-8 x 4628D-11, Table 8, the 2 C Sh Bz wx kernels could be expected to appear following a double crossover in regions 2 and 4 in the male parent. A normal chromatid carrying C Sh Bz wx would result from such a double crossover. The plants arising from these two C sh bz wx kernels were crossed by C sh bz wx, ds, Ac ac male plants. The results of this cross, Table 30, indicate the presence of two normal chromosomes 9 in each plant. No evidence of a Ds locus in the C Sh Bz wx chromosome appeared in either case.

Appendix 4.

Table 14 gives the types of kernels appearing when a Duplication C sh bz Wx Wx Bz Sh Ds/ Normal C sh bz wx, Ac Ac plant was crossed to a C sh bz wx, ds ac plant. With regard to genic constitutions of chromosomes 9, four types of gametes could be expected to be produced by the male parent. These are:

Non-crossover chromatids

(1) Dup. C sh bz Wx Wx Bz Sh Ds

(2) Normal C sh bz wx

Crossover Chromatids

(3) Dup. C sh bz wx Wx Bz Sh Ds

(4) Normal C sh bz Wx

The genic constitution of the chromosomes 9 of seven plants arising from the C Bz-C bz, Sh-sh, Wx-wx kernels of Table 14-a were tested. 96 to 98 percent of the plants arising from these kernels should have the constitution Dup. C Sh bz Wx Wx Bz Sh Ds/Normal C sh bz wx, Ac ac. All seven tested plants had this constitution. Six plants were crossed by C sh bz wx, ds ac plants, Tables 31-a. All seven plants were crossed to C sh bz wx, ds ac plants, Table 31-b, One plant was crossed to a c sh Bz wx, ds ac female plant, Table 31-c.

Two kernels in Table 14-a were classified as possible C Sh bz wx kernels. Such phenotypes were not expected in this cross. To determine if Sh was actually present, plants were grown from these two kernels and self-pollinated. The self-pollinated ears showed only C sh bz wx kernels. The Sh classification in Table 14-a is therefore erroneous, as anticipated. These two kernels should be moved to the last column in Table 14-a.

Appendix 5.

In Table 16-b, which gives the types of kernels appearing from the crosses of c sh Bz wx, ds ac female plants by a Dup. C Sh Bz Wx Wx Bz Sh Ds, Ac Ac plant, a single aberrant kernel was observed. It was colorless and showed Sh → sh and Wx → wx variegation This kernel was sown in the summer of 1949 and the plant arising from the kernel was crossed to a C sh bz wx, ds ac plant and a c sh Bz wx, ds ac plant. The types of kernels appearing on the two resulting ears indicated that this plant had the constitution I Sh Bz wx Ds Ac/ c sh Bz wx ds ac. This constitution could not have been produced by plant 4628L-1. The aberrant kernel in Table 16-b, therefore, represents a pollen contamination and should be removed from this table.

Appendix 6.

In the crosses of C sh bz wx, ds ac plants by Dup. C sh bz Wx Wx Bz Sh Ds/Normal C sh bz wx plants, Tables 14-a, 15-a and 15-c, a few C sh bz Wx kernels appeared. These were interpreted to arise from crossovers as indicated in the supplements to these tables. They should have two normal chromosomes 9. Plants from seven such kernels were examined cytologically and all seven showed two morphologically normal chromosomes 9. Two of the plants were self-pollinated, Table 32-a, and two were crossed by C sh bz wx plants, Table 32-b, and one was crossed to C sh bz wx, Table 32-c. The expected ratios for Wx and wx were obtained.

Appendix 7.

In the cross of a c sh Bz wx, ds ac female plant by plant 4628L-2 which had the constitution Dup. C sh bz Wx Wx Bz Sh Ds/normal C sh bz wx, Ac ac, an aberrant kernel appeared. This cross is not given in the April 1949 report but is similar to that recorded in Table 17-b. This exceptional kernel was colorless and showed Sh-sh, Wx-wx variegation. A plant was grown from this kernel and crossed to a C sh bz wx, ds ac plant, Table 33-a, and by a C sh bz wx, ds ac plant, Table 33-b. These tests showed that the plant carried a Duplication chromosome 9 with C sh bz Wx Wx Bz Sh Ds. The phenotypic appearance of the kernel from which this plant arose may have been produced following an early spontaneous break that deleted the C locus and initiated the breakage-fusion-bridge cycle that produced the Sh-sh, Wx-wx variegation.

Appendix 8.

In order to obtain plants having a chromosome 9 with I Ds Sh Bz Wx, Ac ac, I Bz→C Bz→C bz, Sh Wx kernels were selected from the ear of a C Sh bz Wx/c sh bz Wx, ac ac female plant by plant 4628G-2 that was I Ds Sh Bz wx/C sh bz wx, Ac ac. Two plants arising from such kernels were crossed to C sh bz wx, ds ac female plants, Table 34. The supplement to Table 34 indicates the types of kernels that should appear following crossing-over. Crossing-over in region 3 gave the desired constitution: I Ds Sh Bz Wx. In these kernels, the C Bz areas were variegated for C bz and the majority of these latter areas were Wx-wx variegated. This is the expected variegation pattern that should be produced from dicentric formations at the Ds locus, immediately to the right of the I locus, which initiates breakage-fusion-bridge cycles.

In these crosses, there were 6 C Bz-C bz, Sh-sh, wx kernels. Such phenotypes could arise from crossovers in region 1. It is possible, however, to obtain such phenotypes from I Ds Sh Bz wx chromatids if a Ds event or events occurs early enough to eliminate the I locus from all of the aleurone cells. This occurs in a small fraction of kernels when Ds mutations take place early in development. Plants arising from all 6 kernels would need to be tested to determine whether or not crossing-over in region 1 or early loss of I following Ds mutations were responsible for the appearance of the C Bz-C bz, Sh-sh, wx phenotype.

Appendix 9.

The position of Ds in this case of transposition is definitely between I and Sh. That it is close to the I locus has been apparent from various crosses previously described. Calculations of the crossing-over between I and Ds (see page 16) gave a percentage of 0.74. This value was derived from the frequency of the C Bz-C bz kernels in the crosses of C sh bz wx, ds ac female x I Ds Sh Bz wx/ C sh bz wx, Ac ac male (Table 11-a).

Tests for the presence of Ds in the C Bz chromosome of plants arising from C Bz- C bz kernels of tables 11a and 12-b, and the C-c kernels of table 11-b and 13-c, were conducted by growing plants from these kernels and testing for the presence of Ds. Twelve kernels were selected from variegated kernels, some from the crosses entered in Tables 11-a, 12-b and 13-c, and some from crosses not recorded in the April 1949 report. Two kernels that were doubtful variegates were likewise selected and the plants grown from them tested for Ds. The various selections are given in the accompanying scheme, Scheme 1.

(Insert Scheme 1, page 43)

Information concerning the origin of the selected kernels, the nature of the variegation, the projected constitution of the derived plant, and the culture number of the plant may be seen from the arrangement in this scheme. The first 10 kernels in the scheme were certain variegates. Nine germinated to give plants and all nine plants were tested for Ds. The last two kernels in the scheme were uncertain variegates. The kernel that gave rise to plant 4885 had

Scheme 1

Cross	Table Reference	Phenotype of selected kernel	Projected constitution of plant arising from kernel	1949 Culture Number
C sh bz wx, ds ac ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂				
4363-14 x 4628G-2	11-a	C Bz-C bz, Sh-sh, wx	C Ds Sh Bz wx / C ds sh bz wx	4884
4462C-12 x 4628G-3	Not in April 1949 report	" " "		4887B
C sh bz wx / c Sh bz Wx ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂ 4358A-2 x 4628G-2	"	C Bz-C bz, Sh-sh, Wx	C Ds Sh Bz wx / C ds sh bz Wx	4883B
		C-c Sh Wx	C Ds Sh Bz wx / c ds Sh bz Wx	4883C
Norm. C sh bz wx / Re. c Sh Bz wx ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂ 4365-3 x 4628H-1	12-b	C Bz-C bz, Sh-sh, wx	C Ds Sh Bz wx / C ds sh bz wx	4890C-1, 4890C-2
		C-c, Sh, wx	Norm. C Ds Sh Bz wx / Re. c ds Sh Bz wx	4890D-1, 4890D-2
c sh Bz wx, ds ac ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂ 4347-22 x 4628G-2	11-b	C-c, Sh-sh, wx	C Ds Sh Bz wx / c ds sh Bz wx	4886 (no germination)
Re. c sh Bz Wx ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂ 4353-2 x 4628G-1	11-b	C-c, Sh-sh, Wx	Norm. C Ds Sh Bz wx / Re. c ds sh Bz Wx	4882
C sh bz wx, ds ac ♀ x I Ds Sh Bz wx / C ds sh bz wx Ac ac ♂ 4684-3 x 4628G-3	11-a	One area only of C Bz-C bz, Sh-sh; wx	Presence of Ds in C Sh Bz wx chromosome uncertain	4885
Re. c sh Bz Wx ds / Norm. C Sh Bz wx Ds ♀ x I Ds sh bz wx / C ds sh bz wx Ac ac ♂ 4380A-8 x 4628I-2 AcAc	13-c	Possible C-c kernel but not certain	Presence of Ds in C sh bz wx chromosome uncertain.	4891

only an area of C Bz - C bz variegation. Tests for Ds were negative. The variegated area in the kernel from which this plant arose may have come from a spontaneous breakage in the chromosome 9 carrying C Sh Bz wx loci in one cell mid-way in development of the kernel. The kernel that gave rise to plant 4891 was not certainly variegated. A few specks that could have been interpreted to be c in phenotype appeared in this kernel. These c specks were suspected to be the result of poor color development. It was thought wise to test for Ds in the plant arising from this kernel. No Ds was present in plant 4891.

The nine plants arising from the ten certain variegated kernels were tested by crossing to (1) C sh bz wx, ds ac, (2) c sh Bz wx, ds ac, and to (3) Rearranged chromosome 9 c sh Wx, ds ac female plants, Tables 35 to 41.

The types of kernels appearing on the ears when plants 4883B and C were crossed to C sh bz wx, ds ac plants are given in Table 35. The presence of Ds to the left of Bz is indicated in the supplement to Table 35. The variegated kernels may be used to obtain the crossover frequencies between Ds and Bz. This gives a frequency of 5.8 percent which is the amount expected if Ds were immediately to the right of the C locus. Plant 4883B was crossed to c sh Bz wx, ds ac female plants giving the kernel types shown in Table 36. A high percent of crossing-over between Ds and wx is to be expected, giving a chromosome with C Ds Sh Wx. When Ac is present, such a chromosome will give C-c variegation in the indicated cross. The c areas should be Wx-wx variegated because of the formation of dicentric chromatids just to the right of the C locus. The presence of Wx-wx variegation was evident in all of the C-c kernels that carried Wx. The presence of Ds to the right of the C locus was indicated by the absence of twin areas with deep color in one area and colorless in its twin area.

Plant 4883C when crossed as a pollen parent to c sh Bz wx, ds ac plants, gave the kernel phenotypes entered in Table 37. Crossing-over between Ds and wx, based on the C-c kernels, was 29.4 percent. The data entered in Tables 35, 36, and 37 are consistent in placing the Ds locus immediately to the right of the C locus. It may be concluded, therefore, that the kernel giving rise to plant 4883B and plant 4883C received a chromosome 9 that was derived from a crossover between I and Ds that had occurred in the I Ds/C ds pollen parent plant (Table 11-a).

The projected constitution of plants 4884, 4887B, 4890C-1 and 4890C-2 was C Ds Sh Bz wx/C sh bz wx, Ac ac. These plants were crossed to plants that were c sh Bz wx, ds ac in constitution. Plants 4884B, 4887B, and 4890C-1 had the expected genic constitution as shown in Table 38. Plant 4890C-2, however, had the constitution I Sh Bz wx/C sh bz wx. No Ds locus was evident. Heterofertilization could account for the discrepancy in kernel and plant phenotypes but the absence of Ds events in the I Sh chromosome of the plant arising from this kernel suggests that a Ds event occurred in the division of the sperm that eliminated Ds from one chromatid (sperm fusing with egg) and initiated the breakage-fusion-bridge cycle in the sister chromatid (sperm entering the endosperm nucleus). The data from the three plants, entered in Table 38, allow the position of Ds in these plants to be calculated. Only the variegated kernels may be used to calculate the crossover percentage between Ds and Sh. The value is 4.5 percent. This is the value expected if Ds is very close to the C locus. It is concluded that these three plants received a chromosome 9 derived from a crossover between I and Ds that placed Ds close to the C locus.

Plants 4890D-1 and D-2 were given the constitutions projected in Scheme 1 (page 43): Normal chromosome 9 with C Ds Sh Bz wx/ Rearranged chromosome 9 with c sh Bz wx, Ac ac. The projection for plant 4882 was normal chromosome 9 with C Ds Sh Bz wx/rearranged chromosome 9 with c Sh Bz wx, Ac ac. If each of these three plants were crossed to plants homozygous for c and sh and had no Ac, C to c variegated kernels should appear ~~xxxxxxthexkernels~~ on the resulting ears. Because of the presence of the rearranged chromosome 9 in these three plants, the position of Ds in the homologous normal chromosome 9 could not be determined by crossover techniques. The presence of a Ds locus in half of the C carrying kernels (those that have Ac) is evident, however, in the crosses of these plants to plants that were homozygous c sh Wx, ds ac, Table 39. Plants 4882 and 4890D-1 were each crossed to a plant homozygous for c sh wx, ds ac. The results of this test are those expecte, Tables 40 and 41.

None of the data in Tables 35 to 41 gives evidence that allows a determination of the closeness of the Ds locus to the C locus. Tables 9, 11-a, 11-b, and 12-a, however, do show that this transposed Ds is located very close to the I locus. From these tables, the estimated crossing-over between I and Ds is approximately 0.5. The data in Table 34 project [redacted] of approximately 2 percent. This value is much higher than the calculated values from the data in any one of the other mentioned tables. However, several of the six kernels showing a C Bz → C bz phenotype (projected crossovers) in Table 34 may not reflect crossovers ~~may have lost~~ the I locus may have been lost as the consequence of a Ds event that removed the I locus from one or both sperm nuclei. It will be necessary to test the constitutions of the chromosomes 9 in plants arising from each of these kernels in order to determine the reason for the phenotypic expression of each. The combined data indicate, however, that Ds lies to the right of I (proximal) and very close to it.

Table 21-a

C sh bz wx, ds ac ♀ x Dup. I Ds[1] Sh Bz Wx Wx Bz Sh Ds[2] Ac ac, Ac ac ♂
Norm. C sh bz wx

Kernel type	4805B-19 x 4876A-1	4805B-25 x 4876A-1	4807-1 x 4876A-3	4807-8 x 4876A-3	4803-23 x 4876A-4	4803-27 x 4876A-4	4804-10 x 4876A-5	Totals
I Sh Wx	23	37	7	7	33	22	22	151
I Bz - C Bz - C bz, Sh, Wx-wx	111	102	23	28	50	34	82	430
I Sh wx	10	15	7	6	15	17	28	98
I Bz - C Bz - C bz, Sh wx	21	21	16	21	30	26	60	195
I bz - C bz, Sh wx	4	8	4	1	2	2	1	22
I sh wx not obv. var.	4	4	4	4?	6	3	4	29
I bz - C bz, sh wx	5	5	4	0	9	7	3	33
C Sh Bz Ws not obv. var.	15	13	4	7	20	9	13	81
C Bz - C bz, Sh, Wx-wx	26	37	4	14	17	15	19	132
C sh bz wx	201	149	60	76	158	129	254	1027
Odds	1 C Sh Bz wx	0	0	1 C Sh Bz wx	1 C Sh Bz wx (var.?)	1 C Sh Bz wx	2 C sh bz Wx	6
Totals	421	391	133	165	341	265	488	2204

796 Wx : 1408 wy

Supplement to table 21-a

1 2 3 4 5

I Ds Sh Bz Wx . Wx Bz Sh Ds[2]

C ds Sh bz wx .

Non-crossovers:

Dup. I Ds Sh Bz Wx Wx Bz Sh Ds
- 3 Ac = I - C Bz - C bz Sh Wx-wx = 430 (with reg. 4 + doubles)
- 1 ac = I Sh Wx " " " = 151

Norm. C ds sh bz wx Ac & ac = C sh bz wx = 1027

<u>Region 1</u>

Norm. I ds sh bz wx Ac & ac = I sh wx

Dup. C Ds Sh Bz Wx Wx Bz Sh Ds
- 3 Ac = C Bz - C bz Sh Wx-wx (bz areas Wx-wx or wx)
- 1 ac = C Sh Bz Wx

<u>Region 2</u>

Norm. I Ds sh bz wx
- 3 Ac = I bz - C bz sh wx = 33
- 1 ac = I sh wx

Dup. C ds Sh Bz Wx Wx Bz Sh Ds[2]
- 3 Ac = C Bz - C bz Wx Wx-wx (bz areas wx)
- 1 ac = C Sh Bz Wx

<u>Region 3</u>

Norm. I Ds Sh bz wx
- 3 Ac = I bz - C bz Sh wx = 22
- 1 ac = I Sh wx

Dup. C ds sh Bz Wx Wx Bz Sh Ds
- 3 Ac = C Bz - C bz Sh Wx-wx (bz areas wx)
- 1 ac = C Sh Bz Wx

<u>Region 4</u>

Norm. I Ds Sh Bz wx
- 3 Ac = I Bz - C Bz - C bz Sh wx = 195
- 1 ac = I Sh wx

Dup. C ds sh bz Wx Wx Sh Bz Ds
- 3 Ac = C Bz - C bz Sh Wx-wx (bz areas wx)
- 1 ac = C Sh Bz Wx

Supplement to table 21-a (continued)

<u>Region 5</u>

Norm I Ds Sh Bz Wx	3 Ac = I Bz - C Bz Sh Wx-wx
	1 ac = I Sh Wx
Dup. C ds sh bz wx Wx Bz Sh Ds	3 Ac = C Bz - C bz Wh Wx-wx (bz areas wx)
	1 ac = C Sh Bz Wx

Double crossovers

<u>Regions 2 + 3</u>

Norm. C ds Sh Bz wx Ac + ac	= C Sh Bz wx	=	4
Dup. I Ds sh bz Wx Wx Bz Sh Ds	3 Ac = I Bz - C bz Sh Wx-wx		
	1 ac = I Sh Wx		

<u>Regions 4 + 5</u>

Norm. C ds sh bz Wx Ac + ac	= C sh bz Wx	=	2
Dup. I Ds Sh Bz wx Wx Sh Bz Ds	3 Ac = I Bz - C bz Sh Wx-wx		
	1 ac = I Sh Wx		

Supplement to table 21-a (continued)

Normal chromatids

Non-cross-over	=	1027 C sh bz wx	
Regions 1 + 2	=	62 I sh wx	= I to Sh
Regions 3 + 4	=	315 I Sh wx	= Sh to Wx
Regions 2 + 3	=	4 C Sh Bz wx	
Regions 4 + 5	=	2 C sh bz Wx	
Totals		1410	

% cross-overs region I to Sh = 4.6% (see Table 20 in Report, April, 1949 = 4.7%)

% " " " Sh to Wx =22.48%

Conclusion:

Presence of Duplication does not interfere with the normal amount of crossing over in the region between I and Wx of the distal segment.

Ratio of 2, 3 and 4 from variegated kernels with I

Region 2 = 33 I bz - C bz sh wx

Region 3 = 22 I bz - C bz Sh wx

Region 4 = 195 I Bz - C Bz - C bz Sh wx

Ratios = 1.5 : 1 : 9

Table 21-b

C sh bz wx, ds ac ♀ x Dup. <u>I Ds^1 Sh Bz Wx Wx Sh Ds^2</u> Ac ac ♂ (main)
Norm. C sh bz wx and
Ac ac Ac ac (tiller) ♂

Kernel type	Pollen from main stalk 4806-7 x 4876A-2	Pollen from tiller 4806-4 x 4876A-2	Totals
I Sh Wx (not obv. var.)	41	32	73
I Bz - C Bz - C bz, Sh, Wx-wx	42	50	92
I Sh wx	37	28	65
I Bz - C bz - C bz, Sh wx	39	42	81
I sh wx (not obv. var.)	12	7	19
I bz - C bz, sh wx	9	4	13
I bz - C bz, Sh wx	4	3	7
C Sh Bz Wx	25	15	40
C Bz - C bz, Sh wx	31	29	60
C sh bz wx	184	105	289
Odds	1 C Sh Bz wx	1 C Sh Bz wx 1 C sh Bz wx	3
Totals	425	317	742

205 Wx : 537 wx

Table 21-c

c sh Bz wx, ds ac ♀ x Dup. I Ds Sh Bz Wx Wx Bz Sh Ds
Nor. C sh bz wx

Ac ac, Ac ac ♂

Kernel type	4785-9 x 4876A-1	4785-15 x 4876A-1	4786-75 x 4876A-4	Totals
I Sh Wx (no obv. wx spots)	22*	25*	23*	70
I(-c), Sh,Wx-wx	37	61	45	143
I sh wx	14	10	10	34
I Sh wx	48	49	37	134
C Sh Wx	5	14	8	27
C-c, Sh, Wx-wx	22	31	15	68
C sh wx	169	175	88	432
Odds	0	1 C Sh wx non-var.	0	1
Totals	317	366	226	909

* Some probably I Ds Ac but no losses to give wx during dicentric formation

Summary:

[308 Duplication (minus few c.o. 4) (W+) : 601 normal (plus few c.o. 4) (w+)]

Supplement to table 21-c

1 2 3 4 Ac Ac Ac Ac

I Ds Sh Bz Wx Wx Bz Sh Ds^2

c ds sh bz wx

Non crossovers

Dup. I Ds Sh Bz Wx Wx Bz Sh Ds — 3 Ac = I-c Sh Wx-wx
— 1 ac = Sh Wx non-var.

Norm. C ds sh bz wx Ac & ac = C sh wx non-var. = 432

<u>Region 1</u>

Norm. I sh wx Ac & ac = I sh wx

Dup. C Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 — 3 Ac = C-c Sh Wx-wx (c areas Wx-wx or wx)
— 1 ac = C Sh Wx non-var.

<u>Region 2</u>

Norm. I Ds sh wx Ac & ac = I sh wx

Dup. C ds Sh Bz Wx Wx Bz Sh Ds^2 — 3 Ac = C-c Sh Wx-wx (c areas wx)
— 1 ac = C Sh Wx non-var.

<u>Region 3</u>

Norm. I Ds Sh wx — 3 Ac = I(-c) Sh-<u>sh</u> wx (deficient classification)
— 1 ac = I Sh wx

Dup. c ds sh Wx Wx Sh Ds^2 — 3 Ac = C-c Sh Wx-wx (c areas wx)
— 1 ac = C Sh Wx non-var.

<u>Region 4</u>

Norm. I Ds Sh Wx — 3 Ac = I(-c) Sh Wx-wx
— 1 ac = I Sh Wx

Dup. C ds sh Wx Wx Sh Ds^2 — 3 Ac = C-c Sh Wx-wx (c areas wx)
— 1 ac

Regions 2 + 3

Norm. C Sh wx Ac & ac = C Sh wx non-var.

Normal chromatids:	Non c.o.	= 432	= C sh wx	
	Reg. 1+2	= 34	= I sh wx	c.o. I to Sh = 5.8%
	Reg. 3	= 134	= I Sh wx	" Sh to Wx = 22.4%
	Reg. 2+3	= 1	= C Sh wx	
	Total	601		

Table 22

Dup. I Ds^1 Sh Bz Wx Wx Bz Sh Ds^2 ♀ x C sh bz wx, ds ac ♂

Norm. C sh bz wx

Kernel type	4876A-1 x 4803-27	4876A-2 x 4807-1	4876A-4 x 4804-11	4876A-5 x 4806-11	Totals
I Sh Wx	117 (58 are I - C Bz-C bz)	110 (52 I-C Bz-C bz)	125	154	506
I Sh wx	22 (8 I -C Bz-C bz)	52 (16 I-C Bz - C Bz Sh)	40	22	136
I sh wx	3	3	10	7	23
C Sh Bz Wx	32 (6 C Bz-C bz)	49	71	29	181
C sh bz Wx	0	0	0	0	0
C sh bz wx	139	128	172	183	622
Odds	0	0	0	0	0
Totals	313	342	418	395	1468

665 I : 803 C   687 Wx = 781 wx   823 Sh : 645 sh

Supplement to Table 22

1 2 3 4

I Ds Sh Bz Wx Wx Bz Sh Ds^2

C ds sh bz wx

Non-crossovers

Dup. I Sh Bz Wx Wx Bz Sh Ds = I Sh Wx

Nor. C ds sh bz wx = C sh bz wx = 622

<u>Region 1</u> (I to Sh)

Dup. C Sh Bz Wx Wx Bz Sh Ds^2 = C Sh Bz Wx

Nor. I sh bz wx = I sh wx = 23

<u>Region 2</u>

Dup. C sh Bz Wx Wx Bz Sh Ds = C Sh Bz Wx

Nor. I Sh Bz wx = I Sh wx

<u>Region 3</u>

Dup. C sh bz Wx Wx Bz Sh Ds = C Sh Bz Wx = 136

Nor. I Ds Sh Bz wx = I Sh wx

<u>Region 4</u>

Dup. C sh bz wx Wx Bz Sh Ds = C Sh Bz Wx

Nor. I Ds Sh Bz Wx = I Sh Wx

C.o. I to Sh = 2.9%

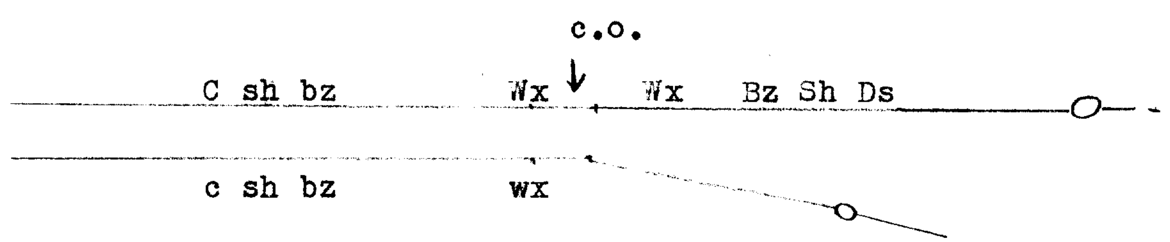
C.o. Sh to Wx = 17.5%

Table 23-a

C sh bz wx ds ac ♀ x $\frac{\text{Dup. C sh bz Wx Wx Bz Sh Ds}^{\text{f.l.}}}{\text{Norm. C sh bz wx}}$ Ac Ac ♂ prob.*

4898-1

Kernel type	4803-19 x 4898-1	4803-24 x 4898-1	Totals
C Sh Bz Wx not obv.var.	49	25	74
C Bz - C bz, Sh, Wx-wx	68	40	108
C sh bz Wx not var.	13	5	18
C sh bz wx	284	145	429
Totals	414	215	629



Normal chromosomes 9:

Non-c.o. = 429
C.o. = 18 = 4.03%

Total = 447

* Ac locus had the "few-late" state. Therefore detection of all of the variegated kernels was not possible.

Table 23-b

Dup. C sh bz Wx Wx Sh Bz Ds^{2} ♀ x C sh bz wx, ds ac ♂

Norm. C sh bz wx
Ac Ac

Kernel type	4898-1 x 4803-27
C Sh Bz Wx*	139
C sh bz Wx non-var.	2
C sh bz wx	120
Total	261

* Variegation class not recorded because of Ac Ac condition in endosperm.

c.o.

C sh bz Wx Wx Bz Sh Ds

C sh bz wx

Normal chromosomes 9:

Non-crossover = 120

C.o. = 2 = 1.63%

Total 122

Table 24-a

C sh bz wx, ds ac ♀ x Dup. C sh bz Wx Wx Bz Sh Ds^2 Ac Ac ♂

Norm. C sh bz wx

4898-3

Kernel type	4804-2 x 4898-3	4804-18 x 4898-3	Totals
C Sh Bz Wx non-var.	18	11	29
C Bz - C bz, Sh, Wx-wx	78	81	159
C sh bz Wx	4	14	18
C sh bz wx	206	357	563
Totals	306	463	769

c.o.

C sh bz Wx ↓ Wx Bz Sh Ds^2

C sh bz wx

Normal chromosomes 9:

Non-crossovers = 563

C.o. = 18 = 3.2%

Total 581

Table 24-b

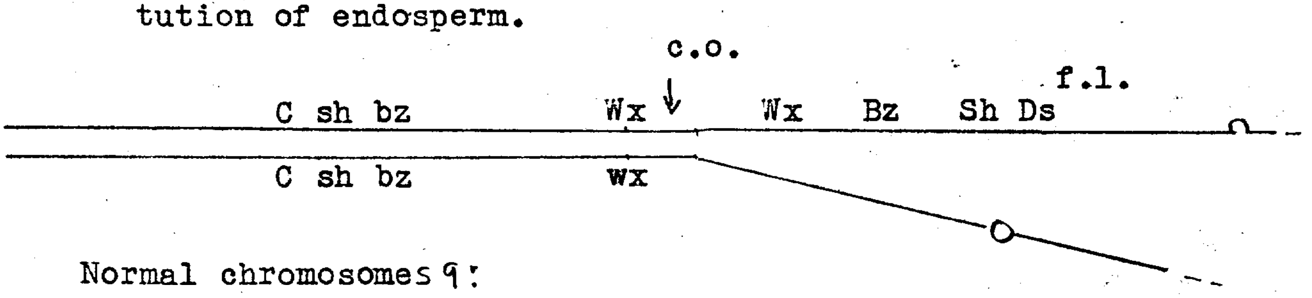
C sh bz Wx Wx Bz Sh Ds^2 ♀ x C sh bz wx, ds ac ♂

C sh bz wx
Ac Ac

4898-3

Kernel type	4898-3 x 4803-38
C Sh Bz Wx*	73
C sh bz Wx non-var.	3
C sh bz wx	63
Total	139

* Variegation class not recorded because of Ac Ac constitution of endosperm.



Normal chromosomes 9:

Non-crossovers = 63

C.o. = $\underline{\ 3\ }$ = 4.5%

Total 66

Table 25-a

Dup. C sh bz Wx Wx Bz Sh Ds^{2}, Ac Ac ♀ x C sh bz wx, ds ac ♂

Norm. C sh bz wx

4898-4

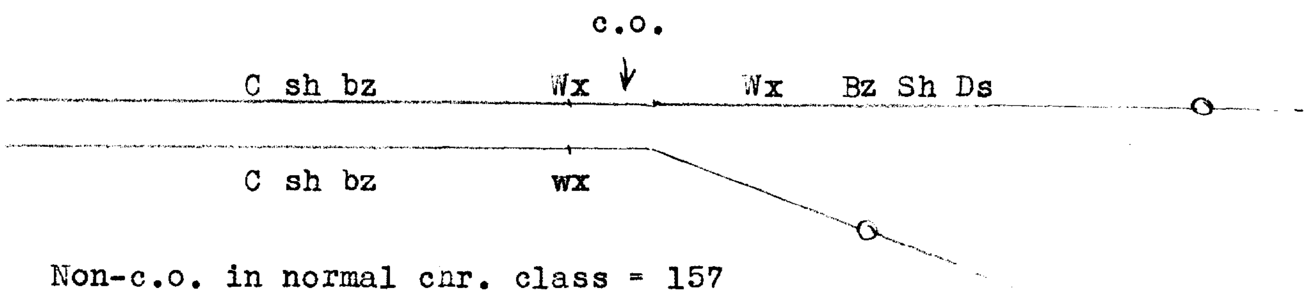
Kernel type	4898-4 x 4804-14
C Sh Bz Wx	24
C sh bz Wx non-var.	0
C sh bz wx	12
Totals	36

Table 25-b

C sh bz wx, ds ac ♀ x Dup. C sh bz Wx Wx Bz Sh Ds^a
Norm. C sh bz wx Ac Ac ♂

4898-4

Kernel type	4803-18 x 4898-4
C Sh Bz Wx not obv. var.	15
C Bz - C bz, Sh, Wx-wx	65
C sh bz Wx non-var.	6
C sh bz wx	157
Totals	253



Non-c.o. in normal chr. class = 157
C.o. 6 = 3.6%

Total 163

Table 26-a

C sh bz wx, ds ac ♀ x Dup. C sh bz Wx Wx Bz Sh Ds$^{f.l.}$ Ac Ac ♂
Norm. C Sh bz wx 4898-2

Kernel type	4801-37 x 4898-2 (tiller)	4803-28 x 4898-2	4805B-22 x 4898-2	4880C-2 x 4898-2	Totals
C Sh Bz Wx (Majority obviously var. C Bz - C bz, Wx-wx)	145	125	154	88	512
C Sh bz wx Non-var.	143	126	121	150	540
C sh bz wx	67	68	75	64	274
C sh bz Wx Non-var.	2	3	2	3	10
C Sh bz Wx Non-var.	3	2	0	1	6
Totals	360	324	352	306	1342

512 Bz : 830 bz

Supplement to table 26-a

Gametes produced by 4898-2

1 2

C sh bz Wx Wx Bz Sh Ds

C Sh bz wx

Non-crossover:

Dup. C sh bz Wx Wx Bz Sh Ds	= C Bz - C bz, Sh, Wx-wx		
Norm. C Sh bz wx	= C Sh bz wx	=	540

Region 1

Dup. C Sh bz Wx Wx Bz Sh Ds	= C Bz - C bz, Sh, Wx-wx		
Norm. C sh bz wx	= C sh bz wx	=	274

Region 2

Dup. C Sh bz wx Wx Bz Sh Ds	= C Bz - C bz, Sh, Wx-wx		
Norm. C sh bz Wx	= C sh bz Wx	=	10

Regions 1 + 2

Dup. C sh bz wx Wx Bz Sh Ds	= C Bz - C bz, Sh, Wx-wx		
Norm. C Sh bz Wx	= C Sh bz Wx	=	6
	Total	=	830

Cross-over percentages based upon the population of recovered normal chromosomes:

	Kernels		Per cent crossing-over
C. o. Region 1	274+6 = 280	=	33.7%
C. o. Region 2	10+6 = 16	=	1.9%
C. o. Regs. 1+2	6	=	0.72%

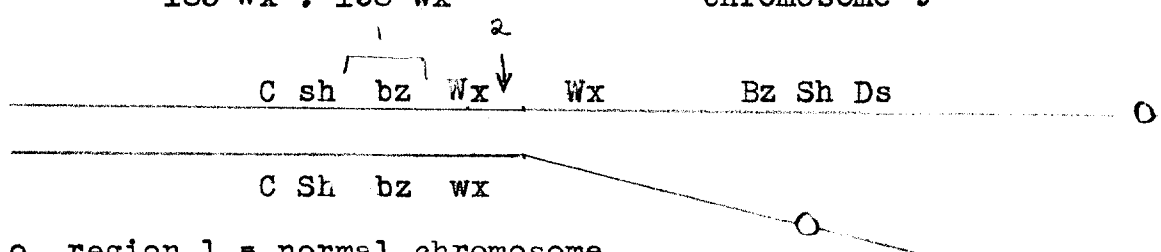
Table 26-b

Dup. C sh bz Wx Wx Bz Sh Ds
Norm. C Sh bz wx
  Ac Ac ♀ x C sh bz wx, ds ac ♂

4898-2

Kernel type	4898-2 x 4803-27
C Sh Bz Wx (Some obviously variegated)	180
C Sh bz wx	120
C sh bz Wx	3
C sh bz wx	38
Totals	341

Summary = 180 Bz : 161 bz No selection against duplication
183 Wx : 158 wx chromosome 9



C.o. region 1 = normal chromosome
with C sh bz wx = 38 = 11.1%
C.o. region 2 = ~~genes~~ normal chromosome with C sh bz Wx = 3 = 0.88%

Table 26-c

Yg c sh Bz wx, ds ac ♀ x $\dfrac{\text{Dup. C sh bz Wx Wx Bz Sh Ds}^{\text{f.l.}}}{\text{Norm. C Sh bz wx}}$ Ac Ac ♂

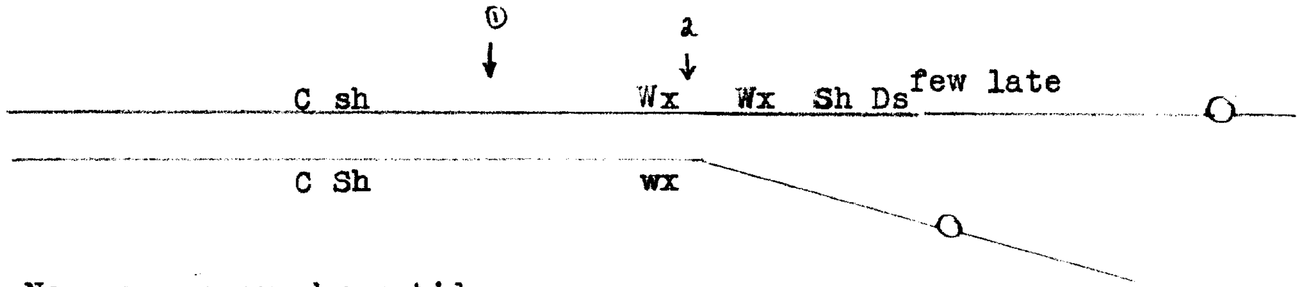
4898-2

Kernel type	4790-21 x 4898-2
C Sh Wx with few small c wx spots	38
C - c, Sh - sh, Wx-wx (c areas wx)	89
C Sh wx non-variegated	83
C sh Wx	2
C sh wx non variegated	58
Totals	270

Summary = 210 Sh : 60 sh

129 Wx : 141 wx

Supplement to table 26-c



Non-crossover chromatids

Dup. C sh Wx Wx Sh Ds, Ac = C-c Sh Wx-wx

Norm. C Sh wx, Ac = C Sh wx = 83

C. o. Region 1

Dup. C Sh Wx Wx Sh Ds, Ac = C-c Sh Wx-wx

Norm. C sh wx, Ac = C sh wx = 58

C.o. Region 2

Dup. C sh wx Wx Sh Ds f.l.,Ac= C-c Sh wx-wx

Norm. C sh Wx Ac = C sh Wx = 2

Crossing-over percentages based on normal chromosomes =

Total = 143

Cross-overs, Region 1 = 58 = 40.5%

" " " 2 = 2 = 1.3%

Table 27-a

Dup. C sh bz Wx Wx Bz Sh Ds
Ac ac ♀ x C sh bz wx, ds ac ♂
Norm. C sh bz wx

Kernel type	4877C-7 x 4807-1	4878D-2 x 4804-11	Totals	4878D-5 4804-11
C Sh Bz Wx (not classif. for var.)	229	190	419	155
C sh bz Wx	2	2	4	0
C sh bz wx	230	170	400	148
Totals	461	362	823	303

Table 27-b

C sh bz wx, ds ac ♀ x Dup. C sh bz Wx Wx Bz Sh Ds Ac ac ♂
Norm. C sh bz wx

Kernel type	4805B-23 x 4877C-5
C Sh Bz Wx not obviously var.	57
C Bz - C bz, Sh, Wx-wx (bz areas wx)	35
C sh bz Wx	0
C sh bz wx	239
Totals	331

Table 27-c

c sh Bz wx, ds ac ♀ x $\frac{\text{Dup. C sh bz Wx Wx Sh Bz Ds}}{\text{Norm. C sh bz wx}}$ Ac ac

Kernel type	4785-11 x 4877C-5	4785-86 x 4877C-5	4785-24 x 4877C-6	4969-11 x 4878D-6	Totals
C Sh Wx non-var.	51	67	92	57	267
C-c, Sh, Wx-wx (c areas wx)	38	60	59	35	192
C sh Wx non-var.	3	4	8	0	15
C sh wx	278	230	200	239	947
Totals	370	361	359	331	1421

Table 27-d

Dup. C sh bz Wx Wx Bz Sh Ds
Ac ac, self-pollinated
Norm. C sh bz wx

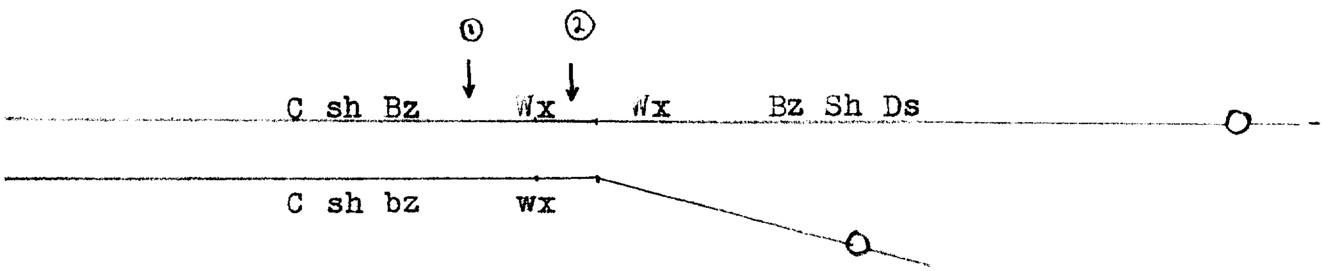
Kernel type	4877C-4	4878D-6	Totals
C Sh Bz Wx (not classified for var.)	351	362	713
C sh bz Wx	6	4	10
C sh bz wx	206	185	391
Totals	563	551	1114

Table 28

Dup. C sh Bz Wx Wx Bz Sh Ds ♀ x C sh bz wx, ds ac ♂

Norm. C sh bz wx
Ac ac

Kernel type	4878D-1 x 4804-11
C Sh Bz Wx (not exam. for var.)	166
C sh bz wx	162
C sh Bz Wx, non-var.	1 (cross-over, region 2)
C sh Bz wx, non-var.	27 (cross-overs, region 1
Totals	356



Among C sh kernels = normal chromosome 9

Non-c.o. = 162

Reg. 1 = 27 = 14.2%

Reg. 2 = 1 = 0.52%

Totals 190

Table 29

I Ds Sh Bz wx
C sh bz wx   Ac ac ♀ x C sh bz wx, ds ac ♂

Kernel type	4877A-1 x 4807-1	4877A-6 x 4807-1	Totals
I Sh* Not obviously var.	113	25	138
I Bz - C Bz - C bz, Sh	87	17	104
I sh* Not obviously var.	4	1	5
C Sh Bz	4	1	5
C sh Bz	0	1	1
C sh bz	220	35	255
Totals	428	80	508

* Probably includes some I bz - C bz var. but bz areas not recognized in Ac Ac ac constitutions.

Table 30

$\frac{\text{C Sh Bz wx}}{\text{C sh bz wx}}$ ♀ x C sh bz wx ds, Ac ac ♂

Kernel type	4877E-1 x 4809-10	4877E-2 x 4809-10	Totals
C Sh Bz, non-var.	217	193	410
C sh Bz, non-var.	12	5	17
C Sh bz	10	3	13
C sh bz	230	193	423
Totals	469	394	863

C.o. Sh to Bz = 3.47%

Table 31-a

Plants from C Bz - C bz, Sh-sh, Wx-wx kernels of 4892 x C sh bz wx, ds ac ♂

Dup. C sh bz Wx Wx Bz Sh Ds ac ac ♀

Norm. C sh bz wx

Kernel type	4892B-1 x 4804-21	4892B-2 x 4804-21	4892B-3 x 4804-21	4892B-5 x 4804-21	4892C-1 x 4804-7	4892C-3 x 4804-7	Totals
C Sh Bz Wx var. and non-var.	310	186	261	172	188	128	1245
C sh bz Wx	4	2	4	1	0	1	12
C sh bz wx	334	205	253	132	216	117	1257
Totals	648	393	518	305	404	246	2514

Table 31-b

C sh bz wx, ds ac ♀ x $\frac{\text{Dup. C sh bz Wx Wx Bz Sh Ds}}{\text{Norm. C sh bz wx}}$ Ac ac ♂

4892 culture

Kernel type	4804-7 x 4892B-3	4804-22 x 4892C-1	4801-30 x 4892C-3	4801-32 x 4892C-3	4804-28 x 4892C-3	4803-48 x 4892C-3	Totals for 4892C-3	Grand totals
C Sh Bz Wx Non-var.	26	64	34	47	40	29	150	240
C Bz - C bz, Sh-sh, Wx-wx (bz areas wx)	35	46	37	53	45	29	164	245
C sh bz Wx Non-var.	2	3	4	2	1	1	8	13
C sh bz wx	211	197	200	208	79	159	646	1054
Totals	274	310	275	310	165	218	968	1552

Table 31-c

c sh Bz wx, ds ac ♀ x Dup. C sh bz Wx Wx Bz Sh Ds / Norm. C sh bz wx Ac ac ♂

Kernel type	4785-82 x 4892C-6
C Sh Wx, non-var.	18
C-c, Sh-sh, Wx-wx (c areas wx)	32
C sh Wx, non-var.	1
C sh wx, non-var.	197
Total	248

Table 32-a

Norm. C sh bz Wx
Norm. C sh bz wx Self-pollinated

Kernel type	4893-1 selfed	4893-3 selfed	Totals
C sh bz Wx, non-var.	129	90	219
C sh bz wx	35	31	66
Totals	164	121	285

Table 32-b

$$\frac{\text{Norm. C sh bz Wx}}{\text{Norm. C sh bz wx}} \; ♀ \; \times \; \text{C sh bz wx} \; ♂$$

Kernel type	4892D x 4803-30
C sh bz Wx	245
C sh bz wx	234
Totals	479

Table 32-e

$$\text{C sh bz wx} \; ♀ \; \times \; \frac{\text{C sh bz Wx}}{\text{C sh bz wx}} \; ♂$$

Kernel type	4901G-6 x 4893-3
C sh bz Wx	124
C sh bz wx	138
Totals	262

Table 33-a

Dup.

C sh bz wx, ds ac ♀ x Dup. C sh hz Wx Wx Bz Sh Ds

Norm. c sh Bz wx normal

Ac ac

Kernel type	4804-29 x 4896
C Sh Bz Wx non-var.	113
C Bz - C bz, Sh, Wx-wx	93
C sh Bz wx	195
C sh bz Wx non-var.	0
C sh bz wx	38
Odds	0
Totals	439

Table 33-b

Dup. C sh bz Wx Wx Bz Sh Ds ♀ x C sh bz wx, ds ac ♂

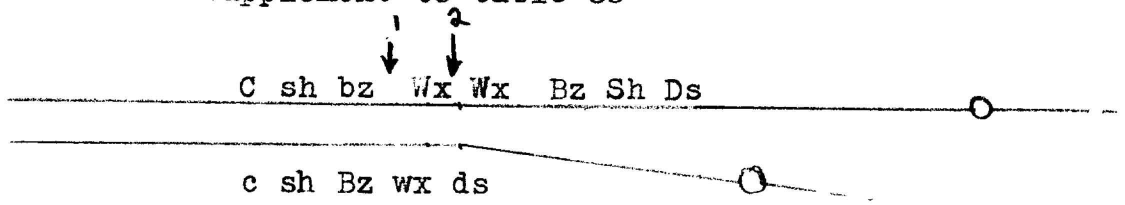
Norm. c sh Bz wx (normal)

Kernel type	4896 x 4803-27
C Sh Bz Wx non-var.	195*
C sh Bz wx	184
C sh bz Wx non-var.	3+
C sh bz wx	17
Odds	0

* 42 were clearly C Bz - C bz Sh Wx-wx

\+ 2 probably not cross-overs but due to deficiency

Supplement to table 33



Non-crossover gametes			F_1 kernel appearance		a	b
Dup. C sh bz Wx Wx Bz Sh Ds	Ac	=	C Bz - C bz, Sh, Wx-wx	observed		
	ac	=	C Sh Bz Wx			
Norm. c sh Bz wx ds (normal)	Ac and ac	=	C sh Bz wx	=	195	184

Region 1

Norm. C sh bz wx ds	Ac and ac	=	C sh bz wx	=	38	17
Dup. c sh Bz Wx Wx Bz Sh Ds	Ac	=	C Bz - C bz, Sh, Wx-wx			
	ac	=	C Sh Bz Wx			

Region 2

Norm. C sh bz Wx ds	Ac and ac	=	C sh bz Wx	=	0	1 prob.
Dup. c sh Bz wx Wx Bz Sh Ds	Ac	=	C Bz - C bz, Sh, Wx-wx			
	ac	=	C Sh Bz Wx			

Table 34

C sh bz wx ds ac ♀ x $\frac{\text{I Ds Sh Bz wx}}{\text{C ds Sh bz Wx}}$ Ac ac ♂

Kernel type	4806-5 x 4883A-1	4880C-3 x 4883A-1	4806-5 x 4883A-2	Totals
I wx	72	76	80	228
I Bz - C Bz - C bz, wx	44	58	80	182
C bz Wx	139	178	173	490
I Wx	27	29	14	70
C Bz wx	9	11	4	24
C Bz - C bz, wx	1	3	2	6
I bz - C bz, Wx-wx (bz areas Wx-wx)	3	4	2	9
I Bz - C Bz - C bz,Wx-wx (bz areas Wx-wx)	21	18	18	57
C Sh bz wx	48	60	40	148
Others	2 C Bz - C bz,Wx-wx*	1 trans- posed Ds= I Sh Bz Ds	1 trans- posed Ds= 1 C Sh bz, Wx-wx*	5
Totals	366	438	415	1219

* Probably from Ds mutation in div. to give sperm = loss of I but not Bz.

C.O. I to Wx (excluding odds) = 25.8%

Supplement to Table 34

C sh bz wx ds ac ♀ x I Ds Sh Bz wx / C ds Sh bz Wx Ac ac ♂

1 2 3
I Ds Bz wx

C ds bz Wx

Non-crossovers

I Ds Bz wx
- Ac = I Bz - C Bz - C bz, wx = 182
- ac = I wx = 228

C ds bz Wx Ac + ac = C bz Wx = 490

<u>Region 1</u>

I ds bz Wx Ac + ac = I Wx

C Ds Bz wx
- Ac = C Bz - C bz, wx = 6*
- ac = C Bz wx

<u>Region 2</u>

I Ds bz Wx
- Ac = I bz - C bz, Wx-wx = 9
- ac = I Wx

C ds Bz wx Ac + ac = C Bz wx

<u>Region 3</u>

I Ds Bz Wx
- Ac = I Bz - C Bz - C bz, Wx-wx = 57
- ac = I Wx

C ds bz wx Ac + ac = C Sh bz wx = 148

Reg. 1 + 3

I ds bz wx Ac + ac = I wx

C Ds bz Wx
- Ac = C ~~Sh~~ bz, Wx-wx = 1
- ac = C bz Wx

Reg. 2 + 3

I Ds bz wx
- Ac = I bz - C bz, wx
- ac = I wx

C ds Bz Wx Ac + ac = C Bz Wx = 0

---

* Several of these probably from germinal losses of I in an I Ds Sh Bz wx chromosome.
Max. c.o. Reg. 1 = 2%

Table 35

C sh bz wx ds ac ♀ x $\frac{\text{C Ds Sh Bz wx}}{\text{C ds Sh bz Wx}}$ Ac ac ♂ (4883B)

or

$\frac{\text{C Ds Sh Bz wx}}{\text{c ds Sh bz Wx}}$ Ac ac ♂ (4883C)

Kernel type	4804-13 x 4883B	4804-27 x 4883B	4801-1 x 4883C	4803-31 x 4883C	4806-2 x 4883C	Totals
C Bz Wx Not obviously var.	12	25	16	14	17	84
C Bz - C bz, Wx-wx (bz areas Wx-wx)	15	18	25	13	16	87
C Bz wx Not obviously var.	61	70	81	56	50	318
C Bz - C bz, wx	60	57	51	44	39	251
C bz, Wx non-var.	123	158	119	124	122	646
C bz, Wx-wx	4	3	5	4	5	21
C bz wx	33	52	29	22	29	165
Odds	0	0	2 C sh Bz wx	0	0	2
Totals	308	383	328	277	278	1574

Summary (minus odds)

740 Bz : 832 bz
838 Wx : 734 wx

Reduced numbers of Bz and wx due to:

Ds mutations in ♂ parent giving deficient chromosome 9

Supplement to table 35

Gametes of 4883B and C

$$\begin{array}{ccccc} & 1 & & 2 & \\ Ds & \downarrow & Bz & \downarrow & wx \\ ds & & bz & & Wx \end{array} \quad Ac\ ac$$

Gametes			Kernel type	
Ds Bz wx	Ac	=	C Bz - C bz, wx	= 251
	ac	=	C Bz wx	= 318
ds bz Wx	Ac + ac	=	C bz Wx	= 646
Region 1				
Ds bz Wx	Ac	=	C bz, Wx-wx*	= 21
	ac	=	C bz Wx	
ds Bz wx	Ac + ac	=	C Bz wx	
Region 2				
Ds Bz Wx	Ac	=	C Bz - C bz, Wx-wx*	= 87
	ac	=	C Bz Wx	= 84
ds bz wx	Ac + ac	=	C bz wx	= 165

$\left.\begin{array}{r} 87 \\ 84 \\ 165 \end{array}\right\}$ Total 336 = 21.3%

* Wx-wx from breakage-fusion-bridge cycles following a Ds mutation giving a dicentric chromatid.

Crossing-over Ds to Bz = 5.2%
Bz to Wx = 21.3%
Ds to Wx = 26.5%

Based on var. kernels

Non c.o.	= 251		
Reg. 1	= 21	=	5.8
Reg. 2	= 87	=	24.2
Total	359		

Table 36

c sh Bz wx, ds ac ♀ $\frac{\text{C Ds Sh Bz wx}}{\text{C ds Sh bz Wx}}$ Ac ac ♂

Kernel type	4785-21 x 4883B	4787-13 x 4883B	Totals
C Sh Wx non-var.	128	142	270
C-c, Sh-sh, Wx-wx (c areas Wx-wx)	20	18	38
C Sh wx non-var.	88	97	185
C-c Sh-sh wx	47	40	87
Odds	1 colorless Sh-sh, Wx-wx	1 c sh wx	2
Totals	284	298	582

308 Wx : 272 wx (minus odds). Reduction in wx class due to Ds mutations in sporophyte of ♂ eliminating the C Ds Sh Bz wx chromosome because of deficiency formation.

30.4% crossing-over Ds to Wx

Supplement to table 36

Gametes formed by 4883B

C Ds wx
Ac ac
C ds Wx

Non-crossover

C Ds wx / Ac = C-c, wx = 87
\ ac = C wx

C ds Wx Ac + ac = C Wx

Crossovers

C Ds Wx / Ac = C-c, Wx-wx = 38 = 30.4% of variegated kernels
\ ac = C Wx

Crossing-over Ds to Wx

C ds wx Ac + ac = C wx

Table 37

$$c\ sh\ wx\ ds\ ac\ ♀\ \times\ \frac{C\ Ds\ Sh\ wx}{c\ ds\ Sh\ Wx}\ Ac\ ac\ ♂$$

Kernel type	4787-20 x 4883C tiller	4786-74 x 4883C main stalk	Totals
C Sh Wx non-var.	15	25	40
C-c, Sh, Wx-wx (c areas Wx-wx)	18	11	29
C Sh wx non-var.	49	61	110
C-c, Sh wx	37	32	69
c Sh Wx non-var.	77	111	188
c Sh wx	31	34	65
Totals	227	274	501

248 C : 253 c

257 Wx : 244 wx

29.4% crossing-over Ds to Wx

Supplement to table 37

		1	2
Gametes from 4883C	C	Ds	wx
	c	ds	Wx

Non cross-Over

C Ds wx < Ac = C-c wx = 69
ac = C wx = 110

c ds Wx Ac + ac = c Wx = 188

<u>Region 1</u>

C ds Wx Ac + ac = C Wx

c Ds wx < Ac = c, Sh-sh, wx (difficult to classify)
ac = c Sh wx

<u>Region 2</u>

C Ds Wx < Ac = C-c, Wx-wx = 29 = 29.4% of C-c kernels
ac = C Wx

about same as distance between C + Wx = 134 gametes in 501= 24.7%

c ds wx Ac + ac = c Sh wx

Table 38

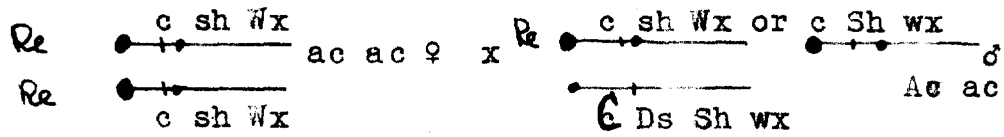
c sh Bz wx ds ac ♀ x $\frac{\text{C Ds Sh Bz wx}}{\text{C ds sh bz wx}}$ Ac ac ♂

Kernel type	4969-15 x 4884	4785-23 x 4884	4786-112 x 4884	4785-8 x 4887B	4793-12 x 4890C-1	Totals
C Sh	131	96	63	89	104	483
C-c, Sh-sh	86	85	96	80	102	449
C sh	207	197	141	192	174	911
C-c sh	1	7	4	5	4	21
Odds	0	1 C-c Sh transp. Ds 1 colorless Sh* 2 c sh wx	1 colorless Sh wx* 1 pec. C-c def.	0	0	6
Totals	425	389	306	366	384	1870

449 C-c Sh : 21 C-c sh = 4.5% crossing over Ds to Sh

* Due to loss of C in sperm from Ds mutation probably.

Table 39



Kernel type	4793-17 x 4882	4793-13 x 4890D-1	4793-14 x 4890D-1	4792-6 x 4890D-2	4793-7 x 4890D-2	Totals
C non-var.	60	98	108	102	57	425
C-c, var.	65	68	94	92	85	404
c	131	191	189	202	139	852
Odds	0		0	0	1 c, Sh-sh, Wx*	1
Totals	256	357	391	396	282	1682

* Probably from loss of C through Ds mutation leaving Sh in chromosome with broken end. Sh-sh due to breakage-fusion-bridge cycle.

Table 40

c sh wx ds ac ♀ x Re $\dfrac{\text{c sh Wx}}{\text{C Ds Sh wx}}$ Ac ac ♂

Kernel type	4786-52 x 4882
C Sh wx non-var.	80
C-c, Sh wx	63
C-c, sh, Wx-wx (c areas Wx-wx)	1
c sh Wx	177
c Sh wx	1
c sh wx	3
Totals	325

Table 41

c sh wx ds ac ♀ x $\dfrac{\text{c Sh wx}}{\text{C Ds Sh wx}}$ Ac ac ♂

Kernel type	4785-4 x 4890D-1
C Sh wx non-var.	35
C-c, Sh wx	32
c Sh wx	80
Totals	147

Table 42

C sh bz wx ds ac ♀ x $\dfrac{\text{I Ds Sh Bz Wx}}{\text{C ds sh bz wx}}$ Ac ac ♂

Kernel Type	5402-9 x 5492-1	5402-10 x 5492-1	5402-12 x 5492-3	5402-14 x 5492-3	5402-17 x 5492-3	5403-67 x 5492-5	5401-68 x 5492-5	5403-71 x 5492-5	5401-1 x 5492-6	5403-10 x 5492-6
I Sh Wx	49	51	89	78	79	59	53	74	46	69
I-C Bz-C bz, Sh-sh Wx-wx	40	42	71	76	76	84	62	86	53	80
I Sh wx	13 Bz 15	15 Bz 20	12 Bz 14	21	14 Bz 15	25 Bz 34	19 Bz 20	29 Bz 42	19 Bz 28	17 Bz 29
I-C Bz-C bz-Sh wx	13	17	12	14	16	27	30	36	29	23
I bz-C bz Sh wx	1	0	1	6	1	3	1	2	1	0
I sh wx	4	2	4	10	7	5	6	11	4	9
I bz-C bz sh wx	7	1	4	2	5	9	6	7	5	2
C Sh Bz Wx	2	8	6	16	9	17	14	14	12	14
C Bz-C bz Sh Wx-wx	0	2	2	0	2	2	0	1	1	2
C sh Bz Wx	3	4	6	6	8	7	7	6	5	13
C sh bz Wx	27	25	37	43	47	84	75	69	47	75
C sh bz wx	85	71	132	116	166	147	126	145	97	156
C Sh Bz wx	1	1	0	1	1	2	3	0	0	0
Odds	0	1 C sh Bz wx	0	1 C sh Bz wx	1	1 I sh Wx	1 C Bz-C bz Sh, wx 1 I sh Wx 1 C sh Bz wx	0	2 I sh Wx	1 C Sh bz Wx 1 I sh Wx

5400-20 x 5494A-1	5400-23 x 5494A-1	5400-50 x 5494A-2	5403-15 x 5494A-2	5404B-25 x 5494A-2	Totals
56	85	36	48	59	931
49	76	61	85	76	1017
16	18 Bz 24	21 Bz 22	14 Bz 15	5 Bz 6	321
18	19	24	17	17	312
2	2	3	1	2	26
3	4	2	2	4	77
2	3	7	4	3	67
4	3	6	1	11	137
0	1	0	1	0	14
5	2	2	4	5	83
24	60	47	34	44	738
101	158	138	96	141	1875
1	0	1	0	1	12
2 I sh Wx 1 C Sh bz wx	2 I sh Wx	1 I bz- C bz sh Wx-wx	0	2 I sh Wx (1 var.)	C sh Bz w: I sh Wx

Table 43

c sh Bz wx, ds ac ♀ x $\frac{\text{I Ds Sh Bz Wx}}{\text{C ds sh bz wx}}$ Ac ac ♂

Kernel Type	5392-68 x 5492-1	5392-13 x 5492-3	5393-9 x 5492-5	5392-23 x 5492-5	5392-45 x 5492-6	5392-37 x 5494A(1)	5393-3 x 5494A(2)	5392-36 x 5494A-2	5392-53 x 5494A-2	Totals
Colorless Sh Wx	82	70	55	49	54	53	22	55	70	510
Colorless Sh, Wx-wx	80	67	54	51	42	51	29	85	81	540
Colorless Sh wx	53	31	49	41	47	47	6	48	32	354
Colorless sh wx	7	9	9	11	17	6	1	7	5	72
C Sh Wx	11	7	18	14	11	8	3	7	2	81
C-c, Sh. Wx-wx (c areas Wx-wx)	0	1	4	0	1	0	0	1	0	7
C sh Wx, non-var.	54	42	80	65	52	40	10	59	53	455
C sh wx, non-var.	143	122	96	110	120	112	46	105	153	1007
Colorless sh Wx	0	0	1	0	0		0	0	2	3
Colorless sh Wx-wx	2	1	0	0	0	1	0	0	0	4
Odds	0	0	0	1 C Sh wx	0	1 C-c Sh wx Ds to left of C	0	0	0	2
Totals	432	350	366	342	344	319	117	367	398	3035

Supplement to table 43

(1)(2)(3)

$$\frac{\text{I}\ \downarrow\ \text{Ds}\ \downarrow\ \text{Sh}\ \downarrow\ \text{Wx}}{\text{C}\ \ \text{ds}\ \ \text{sh}\ \ \text{wx}}$$

Non-crossovers

I Ds Sh Wx	Ac =	colorless Sh-sh, Wx-wx	540
	ac =	colorless Sh Wx	510
C ds sh wx, Ac and ac	=	C sh wx, non-var.	1007

Region 1

I sh wx, Ac and ac	=	colorless sh wx	
C Ds Sh Wx	Ac =	C-c, Sh Wx-wx (c areas Wx-wx)	7
	ac =	C Sh Wx, non-var.	

Region 2

I Ds sh wx, Ac and ac	=	colorless sh wx	72
C ds Sh Wx Ac and ac	=	C Sh Wx, non-var.	81

Region 3

I Ds Sh wx Ac and ac	=	colorless Sh wx (Ac = Sh-sh var.)	354
C ds sh Wx Ac and ac	=	C sh Wx, non-var.	455

Crossing over, regions 1 + 2 = 160 = 5.2%

" " region 1 = 7x4 = 28 = 0.9%

" " region 1, C class = 14

" " region 2, C class = 75